The biology and management of bark beetles in old growth pine forests of Itasca State Park

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Executive summary

From June 1997 through September 1999, we conducted a study of interactions between bark beetles and pine trees in the old growth pine forests of Itasca State Park. The program was initiated in response to severe windstorms in 1996-97 that blew down many large pine trees and led to a dramatic increase in populations of bark beetles within the park. Under some conditions, epidemic populations of bark beetles can overwhelm tree defenses and produce extensive mortality in healthy trees. Consequently, the windstorms created a significant risk for the high-value old-growth forests of Itasca State Park. The objective of our research was to expand knowledge of the bark beetle communities in Itasca State Park, assess patterns of tree resistance and host suitability within the park, evaluate the extent to which bark beetles impact tree survivorship at Itasca, and provide guidance for future management decisions. A complementary research program directed by Dr. Stephen Teale, State University of New York at Syracuse, addressed related issues including the efficacy of beetle control programs.

THE BARK BEETLE COMMUNITY

Pine trees at Itasca Park can be colonized by more than 10 species of bark beetles (Scolytidae), of which the most common are *Ips pini, I. grandicollis,* and *I. perroti*. These three species differ in their relative abundance and life history. Flying adults of *I. grandicollis* are most abundant in May and most of the population seems to have only one generation per year. In contrast, *I. pini* has 2 -3 generations per year at Itasca, and flying adults are most abundant in early September. *I. perroti* has 1 - 2 generations per year at Itasca and flying adults are most abundant in August. During 1998, across 24 trapping stations scattered through the old growth pine forests at Itasca, average cumulative captures for *I. pini, I. grandicollis,* and *I. perroti* were 142, 30, and 16 beetles • trap array $^{-1}$ • year^{-1}. By virtue of having multiple generations per year, *I. pini* has the greatest capacity for rapid increases in population size following blowdowns. Other things being equal, late summer populations of *I. pini* probably represent the greatest threat to pine trees at Itasca. However, the early season flight of *I. grandicollis* may be the greatest threat to trees that have been weakened by winter damage or spring fires. Both *I. pini* and *I. grandicollis* tend to increase in abundance when windstorms blow down suitable host trees. In 1997, the local abundance of *I. pini* was about three-fold higher within sites that sustained blowdowns, but was no higher than background levels at sites 200-300 m away from the blowdowns. In 1998, the abundance of *I. grandicollis* was elevated by about two-fold within blowdowns and at sites 200-300 m away from blowdowns. The restricted spatial scale of population responses to blowdowns indicates that beetle control programs or risk mitigation measures in response to blowdowns could be effective when conducted on a scale of hectares and need not be conducted across many square kilometers. One other practical implication is that forests outside the park suffer little risk of outbreaks due to beetle populations within the park, and vice versa.

Except that they both responded to blowdowns, there was little correlation between the local abundance of *I. grandicollis* and *I. pini,* suggesting that different factors influence their populations, possibly predators. The community includes several specialist predators that might act as natural controls on the abundance of *Ips*. In order of decreasing abundance, these include *Thanasimus dubius* (Coleoptera: Cleridae), *Platysoma cylindrica,* and *P. parallelum* (Coleoptera: Histeridae). All of these predators appear to be univoltine (one generation per year) with the flying adults being most common in May and June. The absence of predators later in the summer must contribute to increased population growth in *I. pini.*

The abundance of predators was positively correlated with the abundance of *I. grandicollis* (perhaps because *I. grandicollis* are the most abundant prey when *T. dubius* adults are feeding and reproducing in May) but negatively correlated with the abundance *I. pini* (perhaps because *T. dubius* predation limits the abundance of *I. pini*). Interspecific competition is another potential control on bark beetle abundance. The three *Ips* species rely on the same food resources, which are frequently limiting. If *I. pini* is the most significant forest pest at Itasca, *I. grandicollis* and *I. perroti* can be thought of as natural control agents of *I. pini.* Alternatively, if *I. grandicollis* is equally likely to attack live trees, then mass-trapping of *I. pini* may allow compensating increases in the

abundance of *I. grandicollis* (because of relaxed competition from *I. pini*) and provide no net benefits in reducing tree mortality.

Three-trap arrays baited with three different combinations of commercially available pheromone blends provide an efficient means of quantifying the abundance of *Ips* and their predators at Itasca. In Chapter 3, we recommend a simple, inexpensive sampling program to monitor year-to-year trends in bark beetle populations at Itasca. This would provide a valuable tool for assessing current risks from bark beetles and adjusting the timing of forest management practices as appropriate. The logistics of this program would be especially easy because of the availability of traps and trained personnel at Itasca.

Appendix 7 is the result of a literature search for scientific papers related to *Ips* bark beetles.

NUTRITIONAL SUITABILITY OF PINE TREES FOR BARK BEETLES

Downed trees of red pine, white pine, and jack pine can all provide excellent habitat for bark beetles. Increases in population size of up to 10-fold per generation are possible (Fig. 1.2). Thus, a local population of 1000 *I. pini* could increase to 1,000,000 *I. pini* over three generations from May to October. A single downed tree could produce as many as 80,000 bark beetles. These data substantiate the concern that blowdowns can lead to rapid dramatic increases in the abundance of bark beetles.

VARIATION IN TREE DEFENSES AMONG SPECIES AND SITES

The primary defense of pine trees against bark beetles is oleoresin, a mixture of monoterpenes and resin acids that flows from wounds and provides a chemical and physical barrier to colonization by beetles. Measurements of resin flow from standardized wounds provide a means for evaluating tree resistance to beetle attack. Of the three species of pine in Itasca, jack pine has extremely low resin flow (most trees have no measurable resin flow) and appears to be most vulnerable to beetles (Fig. 1.1). On average, white pine and red pine have much higher resin flow than jack pine.

Because of the special importance of old growth red pine at Itasca, we explored in detail the patterns of variation in red pine defenses against bark beetles. There was extensive variation among 12 old growth stands of red pine in resin flow and all measurements of tree growth, tree morphology, and stand attributes (Figs. 2.7-2.9). The old growth forest at Itasca is a mosaic of red pine stands that differ in their constitutive defenses against bark beetles and many other attributes as well. We used regression analyses to identify the simplest combinations of parameters that could predict spatial patterns in constitutive resin flow (Fig. 2.10, Tables 2.1-2.2). Average resin flow at a site can be predicted as $Resin = 0.031 \cdot DBH - 0.013 \cdot BA$, where DBH = diameter at breast height in cm and BA = basal area of the stand in m^2 / ha. This relationship explained 74% of the variation among sites in average resin flow. Thus, old growth stands of red pine that are least defended against bark beetles are those with relatively small trees and a high basal area. Such sites deserve the most careful consideration for management strategies to minimize risk from bark beetles (e.g., by removing, debarking, or burning the trunks of large pine trees that have blown down before they can produce bark beetles).

In addition to variation among sites, there were strong differences within sites between trees that were classified *a priori* as belonging to codominant or intermediate crown classes (resin flow averaged 43% higher in codominant vs. intermediate trees; Fig. 2.7). Thus, within a stand, trees of intermediate crown class are least defended against bark beetles.

EFFECTS OF TREE AGE ON GROWTH AND ANTI-HERBIVORE DEFENSES

It has been hypothesized that the old-growth stands of red pine at Itasca are approaching senescence and, as a consequence, have declining levels of defense against insects and pathogens. If so, tree mortality from beetles might be expected to accelerate over the next two or three decades, in which case appropriate management strategies might be different than if the forest could realistically persist through another century.

Overall, there was only a weak tendency for declining growth rates in mature red pines at Itasca (Fig. 2.5). Average radial growth rates held near 1 mm / year for most of this century. A depression in growth rates from 1989-91 corresponds to a drought. There was a slight tendency for older trees to have lower growth rates, but there were no effects of age on physiological stability as measured by interannual variation in growth rate, nor were old trees more likely to be in growth decline than young trees (Fig. 2.6). Furthermore,

older trees suffered less impacts from drought and had higher resin flow than younger trees. These data indicate continuing growth and high defense in even the oldest red pines at Itasca. There was no suggestion of physiological senescence in even the oldest trees in our sample (up to 220 years old). In the absence of mortality from windstorms, bark beetles, fires, lightning, icestorms, and other disturbances, it seems realistic to expect that many mature red pines in Itasca could live for another century or more. This is very positive news for park management. One consequence is that it becomes appropriate to minimize any manageable risks of tree mortality. Given the long potential lifespan of these trees, even very small changes in mortality risk can have dramatic impacts on the lifetime of the forest (see Figs. 5.7 and 6.9 in Chapters 5 and 6).

We further tested the effects of tree age on anti-herbivore defenses by comparing resin flow in mature red pines at Itasca (100 - 220 years old) with young red pines (30 - 80 years old). Mature red pines had dramatically higher resin flow (about two-fold) than younger red pines growing on similar sites in the same area (Figs. 2.11-2.12). These results reinforce the conclusions that mature red pines at Itasca are not senescing and are not poorly defended against bark beetles.

AGE STRUCTURE OF RED PINE FORESTS AT ITASCA

Among 11 stands of mature red pine at Itasca, the oldest median age of establishment was 1819 and the youngest was 1902. Five of 11 stands were even-aged, suggesting that they originated as the result of stand-clearing wildfires, and six contained trees of mixed ages, indicating that stand-clearing fires have not always been required for the regeneration of red pine at Itasca. At these latter sites, we found adjacent trees that differed in age by as much as 50 - 140 years. This is more positive news because it implies that red pine regeneration is possible without the elimination of mature trees.

REGIONAL PATTERNS IN THE SUSCEPTIBILITY OF RED PINE TO BARK BEETLES

Because the forests at Itasca are very near the western distribution limits of red pine, Itasca forests might be chronically stressed and generally susceptible to insects and pathogens. We tested this hypothesis by comparing resin defenses of red pines in Itasca with those growing in a region of west-central Wisconsin where growth rates are near the maximum for red pines anywhere. For comparably aged red pines, resin flow averaged nearly twice as high in Itasca as in Wisconsin (Fig. 2.13). These results are contrary to the hypothesis that trees growing on marginal sites, such as Itasca, tend to be less defended against bark beetles than trees on high quality sites. However, results are completely consistent with a physiological model that predicts secondary metabolism will increase in environments where water deficiencies limit growth more than photosynthesis (Fig. 2.14). It appears that the low growth of red pines at Itasca is associated with increased resin flow and reduced risks from bark beetles, which should increase the potential longevity of the forest. A counterpoint to this good news is that the same physiological model predicts that tree defenses at Itasca could be compromised during droughts. We lack any basis for speculating on the severity of drought that would be required to increase tree risks from bark beetles.

All available data indicate that (1) red pine in Itasca are not chronically susceptible to bark beetles compared to red pine growing on better sites and (2) old red pine at Itasca are not chronically susceptible to bark beetles because of reduced resin flow, declining growth, and senescence. Mortality of Itasca red pines from bark beetles is apparently the product of long exposure to low risks rather than an indication of a forest that is in rapid decline or chronically vulnerable to insects.

EFFECTS OF WINTER TEMPERATURES ON BARK BEETLES

The ability to survive annual temperature minima can be a critical determinant of insect abundance. If winter conditions are a significant source of mortality for *Ips*, then it would be possible to predict population abundance in the upcoming summer as a function of winter temperatures and snow cover, and such models could have high utility for anticipating and mitigating risks of tree mortality from bark beetles. This component of our research was designed to measure the lower lethal temperature of *Ips* spp., identify their overwintering sites, and develop a model to predict winter mortality of *Ips*. The lower lethal temperature for adults of *I. pini*, *I. grandicollis*, and *I. perroti* averaged -12.6, -15.2, and –14.4 °C , respectively (Table 4.1). Larvae and pupae are less cold tolerant than adults and are obliged to

remain within the phloem of their host trees (where they are poorly buffered from temperature extremes). Apparently, the only life stages that can survive most winters are the adults that reach overwintering sites in the forest litter.

We collected microclimatic data to develop a mathematical model that estimates temperatures within the overwintering habitat of *Ips* adults (Eq. 4.1). This allowed us to identify winter conditions that can kill bark beetles (Fig. 4.2). For example, during a cold snap where minimum air temperatures reach -35 °C, with no snow cover, we expect about 65% mortality in *Ips* adults (Fig. 4.3). Such conditions are less common at Itasca than we had expected. Based on climate records from nearby Bemidji, MN, winter mortality of *Ips* adults reached a maximum of only 33% from 1947 - 1992 (compare to a maximum of 71% in west central Wisconsin during the same years; Fig. 4.4). From the perspective of *Ips* bark beetles, Itasca has relatively benign winters because snowfall usually insulates the upper soil well before the coldest annual air temperatures (Figs. 4.6-4.7). Fig. 4.3 provides a tool for predicting *Ips* mortality under any combination of winter air temperature and snow cover.

DO BARK BEETLES KILL TREES AT ITASCA?

Ips infestations at Itasca could be restricted to trees that are destined to die soon anyway. If so, the abundance of *Ips* would have no consequences for the demography of pine forests at Itasca and could be ignored in management decisions. We tested whether or not *Ips* kill red pines at Itasca by surveying for trees that were infested by bark beetles, monitoring the fate of those trees, and evaluating whether the infested trees were in declining physiological condition prior to being infested by beetles. In 1998, we examined about 4000 mature red pines and located 41 that were infested by bark beetles (see photos in Figs. 5.1 and 5.3). In 1999, we searched the same area and found 39 other trees that had come under attack. *Ips pini* and/or *I. grandicollis* accounted for most of the infestations. Of 41 red pines infested during 1998, 21 were dead, or very nearly so, by the end of the next growing season (Fig. 5.3). Of the 17 trees that were still alive, six were sustaining continuing attacks in 1999, and 11 were apparently free of new attacks (Table 5.1). In our judgement, some of the trees in this latter group might survive for decades longer. However, all attacked trees sustained irrepairable damage to their vascular system, lost significant portions of their crown, and were destined to be more vulnerable to future insects, pathogens, fire, and windstorms. Thus, beetle infestations led to rapid mortality in about half of the attacked trees and increased the probability of mortality for the remainder.

None of the trees that were infested by bark beetles showed a pattern of declining growth in the years immediately preceding the infestation nor any systematic differences from their paired control trees at any time from 1935 - 1996 (Figs. 5.4-5.5). In fact, bark beetle infestations included some of the fastest growing trees in the park (Fig. 5.6). Apparently, bark beetles at Itasca commonly kill red pines that could otherwise live for decades. With an annual mortality rate of 0.5% from bark beetles (as suggested by our surveys), and no regeneration of trees, the Itasca population of red pines would be halved by beetle attacks in 139 years. The expected half life of the forest declines to 65 years if we include a modest level of background mortality from other causes (0.25% / year) and assume that the mortality rate increases in trees that have survived past beetle attacks (to 5% / year). If the same hypothetical forest lacked bark beetles, it would have a half life of 277 years. Bark beetle attack rates such as we observed at Itasca can have surprisingly large effects on forest longevity (Fig. 5.7).

INTERACTIONS BETWEEN FIRE, BARK BEETLES, AND TREE MORTALITY

Prescribed fires were implemented at Itasca during 1998 and 1999. We extended our research to consider fire because it appeared that interactions between fire and bark beetles may be at least as important to forest management as interactions between windstorm and bark beetles. Prescribed fires might reduce bark beetle abundance by killing beetles or increase local abundance by producing volatiles that attract beetles. In fact, the 1998 fire had only limited effects on the abundance of bark beetles (slight increases in *I. pini* during May and slight decreases during mid-summer; Fig. 6.1). However, fire produced a short-term reduction in the resin defenses of red pine and triggered rapid colonization of the scorched trunks by bark beetles (Figs. 6.3 - 6.4, Table 6.1). Within 10 - 30 days, the resin flow in scorched trees increased to higher than baseline levels (Figs. 6.2 - 6.3), which restricted the extent of beetle galleries and probably saved many scorched trees from being killed by bark beetles (Fig. 6.4). Nonetheless,

these attacks kill the phloem, interrupt vascular connections, and partially girdle the tree (permanently). The cambium in the infested area also dies, which precludes additional growth of bark or wood and ensures that a scar will form. This is probably the dominant process by which so-called "cat-faced scars" have been produced on mature red pines at Itasca (Fig. 6.5 - 6.6).

Following the prescribed burns in 1998-99, we found dozens of red pines with incipient scars forming as a result of beetles attacking the scorched lower trunks (Fig. 6.4). We also found many red pines with pre-existing cat-faced scars, whose living bark was being colonized by beetles around the periphery of the old scar. This appeared to be the result of greater heat trauma to the living tissue around the region of the trunk that lacked insulating bark. Finally, the prescribed fires directly killed many red pines when the wood that was exposed at pre-existing scars was ignited by the fire (Fig. 6.5). Fires and beetles can produce a positive feedback loop in which fires promote beetle attack, which increases susceptibility to future fires and future beetles, and which eventually leads to the death of the tree (Fig. 6.7). There can be additional positive feedback at the level of the forest, because a tree that dies in one fire increases the fuel load for future fires and therefore increases the probability of fire and beetle damage to adjacent trees (Fig. 6.8).

Because the relationship between fire, bark beetles, and tree mortality appears to involve positive feedbacks, the proportion of trees that succumb to fires would be expected to increase with each additional fire, and it would be easy to underestimate the consequences of future fires for tree mortality. For example, a doubling of tree mortality rates as a result of increased fire frequency could reduce the half-life of the forest from 65 years to 37 years (Fig. 6.9). We suggest that fire management practices at Itasca be developed in concert with the refinement and parameterization of demographic models of tree survivorship. Presumably, the optimal fire management strategy is one that balances the costs of reduced survivorship in mature trees against the benefits of increased regeneration.

Chapter 6 concludes with a list of specific recommendations for minimizing tree mortality associated with fire and bark beetles.

Appendices 1-5 provide additional raw data. Appendices 6 and 7 are two papers from this research that have been accepted for publication in peer reviewed journals (*Environmental Entomology* and *Forest Ecology & Management*). Three additional appendices in Volume II of this report are the result of literature searches for scientific papers related to *Ips* bark beetles, fire and insects, and fire and pine forests, respectively; they include citations and abstracts for about 250 papers.

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Volume II of the report contains three additional appendices:

A bibliography of *Ips* bark beetles

A bibliography of interactions between fire, trees, and insects

A bibliography of fire ecology in coniferous forests

Introduction

In 1994-96, the old growth pine forests in Lake Itasca State Park sustained a sequence of heavy blowdowns from windstorms. The downed trees provided abundant food resources for *Ips* bark beetles and led to a dramatic increase in the abundance of *Ips*. Under some conditions, it is thought that *Ips* are capable of attacking and killing trees that would otherwise survive. Limitations in soil water availability, such as characterize forests near the edge of the Great Plains in western Minnesota, have been hypothesized to exacerbate the risk of tree mortality from bark beetles. Thus, bark beetles pose a potentially severe risk for the remaining old growth forests of Lake Itasca State Park. The objective of this research was to assess that risk, evaluate potential strategies to mitigate the risk, and develop biologically sound models to guide the management of this unique and irreplaceable forest ecosystem. Although there was a substantial pre-existing knowledge base regarding interactions between pine trees and bark beetles, this research was unique in being among the first scientific study of bark beetles in old growth pine forests of the Great Lakes region. Because Lake Itasca represents one of the last remaining patches of primary forest from this once extensive forest type, results also have considerable significance in advancing our understanding of the natural workings of unaltered forest ecosystems. Our research is presented in six chapters.

CHAPTER 1. PATTERNS OF HOST SUITABILITY AMONG PINE SPECIES.
Itasca State Park contains red pine, white pine, and jack pine. All are potential hosts of *Ips* bark beetles, but their relative quality for bark beetles is not known. This chapter compared the anti-herbivore defenses and nutritional suitability of the three species, which has significance for evaluating the consequences of blowdowns in pine stands with different species composition.

CHAPTER 2. GROWTH AND ANTI-HERBIVORE DEFENSES OF RED PINE AT ITASCA STATE PARK.
The physiology of pine trees, and their resistance to bark beetle attack, could be influenced by variation in tree age, water availability, nutrient availability, competition with nearby trees, and other environmental effects. If so, there would be predictable patterns in the susceptibility of pines to beetle attack that could be used to assess risks and guide strategies for monitoring and control. In this component of the research, we tested whether or not mature red pines at Itasca are in a state of declining growth and weakened defenses. We also assessed variation in growth and anti-herbivore defenses among stands to evaluate whether or not there are some stands within the park that have particularly high susceptibility to beetles, and to characterize attributes of such stands for the purposes of developing a system for risk-rating. Finally, we compared the anti-herbivore defenses of red pines in Itasca with red pines growing in sites that are more favorable for tree growth. This allowed us to test if the forests at Itasca are chronically stressed and generally susceptible to insects and pathogens.

CHAPTER 3. BARK BEETLE COMMUNITIES AT ITASCA STATE PARK
Itasca Park potentially harbors three different species of *Ips* bark beetles and a guild of specialist predators that prey upon the bark beetles. We conducted sampling of pine forests with different disturbance histories to evaluate which of the bark beetle species are most common at Itasca, which are most responsive to windstorm disturbance, and whether or not predation and/or competition are likely to function as natural control agents on bark beetle populations. This research was also designed to characterize seasonal patterns of abundance in the various species and assess the efficacy of different pheromones as trap lures.

CHAPTER 4. COLD TOLERANCE AND WINTER MORTALITY OF BARK BEETLES AT ITASCA STATE PARK.
Winter temperatures could be a critical determinant of bark beetle population size at Itasca. If so, then it should be possible to reliably predict population abundance in the upcoming summer as a function of winter temperatures and snow cover. Such models could have high utility for management decisions. This component of the research was designed to: (1) measure the lower lethal temperature of the different species and life stages of *Ips*; (2) identify overwintering sites of *Ips*; and

(3) develop a model that incorporates knowledge of cold tolerance, overwintering sites, and microsite temperatures to predict winter mortality of *Ips* using easily measured climatic parameters.

CHAPTER 5. DO BARK BEETLES KILL TREES AT ITASCA STATE PARK?

Forest entomologists are mixed in their opinions of whether or not *Ips* bark beetles are a significant source of mortality for pine trees in the Great Lakes region. Most dying trees are infested by *Ips*, but this could be because *Ips* cause the death of the tree or simply because *Ips* are efficient at locating and colonizing trees that are dying for other reasons. Which of these scenarios is true has important implications for forest management at Itasca State Park. If *Ips* infestations are restricted to trees that are destined to die with or without the presence of bark beetles, then the abundance of *Ips* has no consequences for the demography of pine forests at Itasca, and there is no compelling reason to monitor bark beetle populations, control them, or make any management decisions based upon the abundance of bark beetles. Alternatively, if *Ips* commonly attack and kill trees that are otherwise healthy, then bark beetles may deserve careful consideration in forest management decisions. We addressed this question by surveying the population of red pines at Itasca for trees that were infested by bark beetles, monitoring the fate of those trees, evaluating whether or not the infested trees were in declining physiological condition prior to being infested by beetles, and developing a simple demographic model to evaluate the potential contributions of mortality from bark beetles on the long term survivorship of red pine forests at Itasca.

CHAPTER 6. INTERACTIONS BETWEEN FIRE, BARK BEETLES, AND TREE MORTALITY

During our bark beetle research at Itasca, prescribed fires began to be implemented as a management tool. Our observations following the fires, and a preliminary review of the literature, suggested the potential for complex interactions between fire and bark beetles at Itasca that may be at least as important to forest management decisions as interactions between windstorm and bark beetles. Therefore, we extended our research by (1) comparing bark beetle abundance in forests that were and were not exposed to prescribed fires, (2) monitoring the fate of trees that were infested by bark beetles after the fire, (3) testing the effects of bark scorching on the resin defenses of trees against bark beetles, (4) characterizing the processes by which fire and bark beetles can interact to influence tree mortality, and (5) expanding the demographic model for pine survivorship from Chapter 5 to incorporate the potential effects of fire and suggest an analytical framework for assessing the costs and benefits of prescribed fire for the long term management of pine populations at Itasca.

Chapter 1
Patterns of host suitability among pine species

1.1 Introduction

There are three potential host species for *Ips* at Itasca: red pine (*Pinus resinosa*), white pine (*Pinus strobus*), and jack pine (*Pinus banksiana*). The relative susceptibility of these species for *Ips* is not known, but is critical in evaluating the risks from bark beetles to existing pine stands. For example, if red pine is generally better defended against bark beetles than jack pine and white pine, then increases in beetle population size for any reason (e.g., a blowdown that provides downed logs for beetle reproduction) would pose a greater threat to standing jack pine and white pine than to red pine. Red pine, white pine, and jack pine could also differ in their nutritional suitability for the reproduction of bark beetles. If so, blowdowns in different pine stands would have different consequences for regional population size of bark beetles.

1.2 Methods

We compared resin flow and phloem thickness of the three tree species at each of two sites where they all co-occurred . We also compared red pine and white pine at an additional two sites where they co-occurred. Resin flow was measured as the mass of resin that flowed within 24 h from standardized wounds (13 mm in diameter) to cambium of the bole at a height of 1.5 m. Phloem discs of the same size were removed, lyophilized, and weighed as a measure of phloem thickness (mg dry mass / 1.23 cm2).

We removed bark samples from the lower, middle, and upper boles of downed trees that were infested by *Ips* during the summer of 1997 (three jack pine, four red pine, two white pine). Careful examination of the *Ips* galleries that were etched in the phloem allowed us to compare the reproductive success of bark beetles among pine species and tree individuals. Sample plots (10 x 10 cm) were selected within each bark sample. Within each bark sample, we selected three maternal galleries; for each gallery, we measured the total length, number of eggs laid by the female, number of galleries started by the larvae, and the number of adult progeny (evident as pupal chambers and emergence holes). Brood survival was calculated as adult progeny / egg. We also measured the total length of maternal galleries within 10 x 10 cm square plots, which provided an estimate of colonization density and allowed us to evaluate of the effects of intraspecific competition on reproductive success.

1.3 Results and Discussion

Average resin flow in red pine and white pine appeared sufficient to resist attacks by small to moderate numbers of *Ips* (Fig. 1-1). In contrast, the resin flow of jack pine was generally very low, suggesting that a majority of the tree population is susceptible to attack by *Ips*. Compared to codominant trees, trees of intermediate crown stature had lower resin flow in two sites for red pine and one site for white pine (Fig. 1-1). White pine had generally higher resin flow than red pine at two sites (LaSalle and No Name), lower resin flow than red pine at a third site (Landmark), and similar resin flow to red pine at a fourth site (East Gate). Phloem thickness, a measure of carbohydrate reserves in the trees and nutritional suitability for beetles, averaged highest among white pine and lowest among jack pine, but most trees of all three species appeared to have adequate phloem to support the development of *Ips* larvae. In white pine, codominant trees had consistently higher phloem thickness than intermediate trees.

In downed trees, reproductive success of *Ips* was highest in jack pine and lowest in white pine (Fig. 1-2). In jack pine, females laid an average of 14 eggs compared to 9-10 eggs in red pine and white pine. Survival of eggs to adult was >50% in jack pine compared to only 25% in white pine. Attack densities were high in downed trees of all 3 species (average of 8-13 galleries / dm2, Fig. 1-2). However, even at these densities there was only a suggestion of inverse density-dependence in the survival of progeny (Fig. 1-3). There was significant variation in the success of *Ips* among trees within species (Fig. 1-3), indicating that tree physiological status can be as important as differences among tree species in influencing beetle success.

Results indicate that downed trees of all three pine species represent suitable habitat for bark beetles. Consequently, windstorms or other disturbances that eliminate tree resistance can promote rapid increases in the population size of bark beetles. Increases of >10-fold per generation are possible. Thus with three generations per year, a local population of 1,000 *I. pini* could increase to 1,000,000 from May to September. A single large pine tree can produce an astonishing number of *Ips*. A tree that is 30 m tall and 70 cm in diameter at breast height contains about 16 m2 of phloem habitat (conservatively assumes that the lower 15 m of the bole is suitable, that the average diameter of the lower bole is 50 cm, and that 70% of the

circumference is colonized). Fig. 1.2 indicates that suitable phloem can produce about 50 *Ips* adults / dm2 (50 cm gallery / dm^2 • 2 eggs / cm • 0.50 survival of eggs to adults). So such a tree might produce 80,000 *Ips* adults.

Populations of all three pine species, but especially jack pine, contain some live trees with such low resin flow that they may be susceptible to infestation by even modest populations of *Ips*. Jack pine stands may provide reservoirs that sustain bark beetle populations during times when they are otherwise rare and would allow rapid growth of beetle populations in the event of windstorms. Consequently, stands of red pine and white pine that are intermixed with jack pine may be at generally higher risk of bark beetle attack. Alternatively, if *Ips* attack jack pine preferentially, jack pine may function like "trap crops" within mixed stands and actually reduce the probability of attacks in red pine and white pine. Knowledge of behavioral preferences of *Ips* for different pine species is needed to distinguished between these very different scenarios.

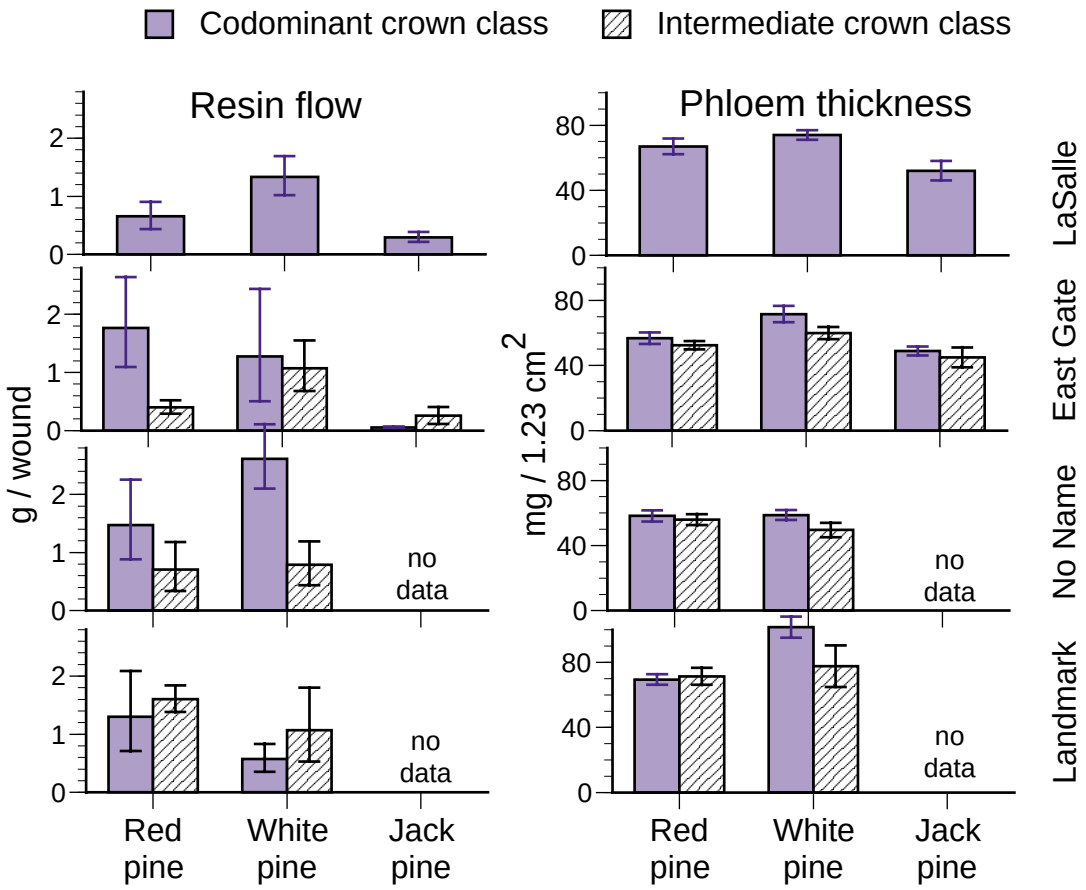

Fig. 1.1. Resin flow and phloem thickness of red pine, white pine, and jack pine at Itasca State Park.

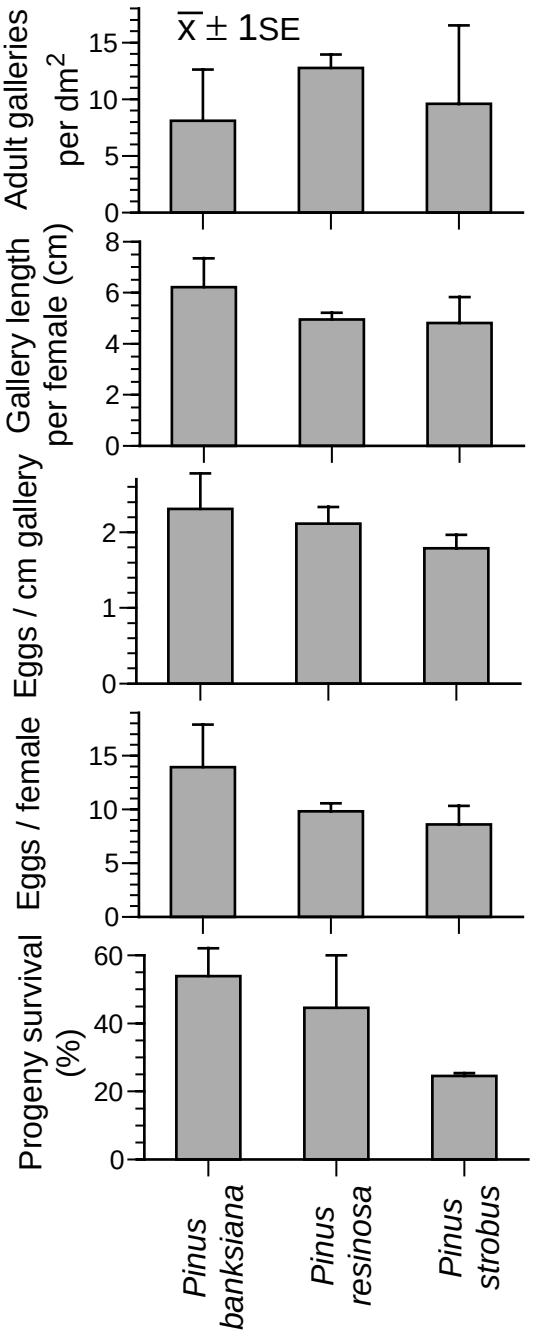

Fig. 1.2. Colonization densities and reproductive success of *Ips* bark beetles in downed trees of three species of pine at Itasca State Park

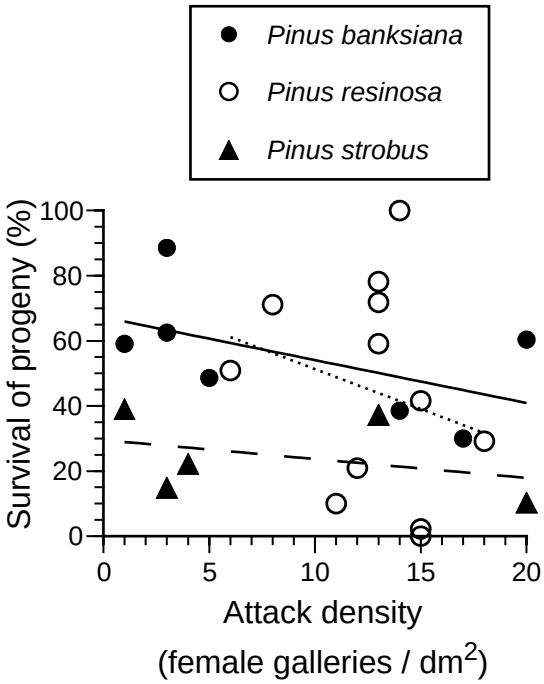

Fig. 1.3. Survival of progeny as a function of attack density for *Ips* bark beetles in downed trees of three species of pine at Itasca State Park

Chapter 2
Growth and anti-herbivore defenses of red pine at Itasca State Park

2.1 INTRODUCTION

The susceptibility of pine trees to bark beetles is influenced by the defensive system of the trees and the abundance of bark beetles. Oleoresin, a mixture of terpenes and resin acids, is the primary defense of pine trees against bark beetles. When the bark of a tree is penetrated, as by a bark beetle, resin tends to be exuded from the wound. This resin presents a physical and chemical barrier to beetles. The pool of oleoresin that is preformed and stored within the vertical resin duct system of the trees function as a constitutive defense. In general, higher levels of constitutive resin flow reduce the success of colonizing beetles (Reeve et al. 1995, Fig. 2.1) and tend to protect the trees. Constitutive resin flow, and therefore the susceptibility of pine trees to bark beetles, can be influenced by environmental conditions, tree age, and tree genetics. In this research, we assessed patterns in the constitutive resin flow of red pines at Itasca. Prior to this research, no studies have measured the levels of constitutive resin flow in red pine, and very little was known about the effects of environment or tree age on the susceptibility of red pines to bark beetles. Most pine trees also have a capacity for inducible defenses. For example, wounding by mechanical damage, beetles, fire, or pathogens can potentially lead to increased synthesis of resin within the resin duct system and contribute to increased resistance to subsequent attacks (Cook and Haine 1987, Popp et al. 1991, Tisdale and Nebeker 1992, Nebeker et al. 1993, Ruel et al. 1998). Responses of the resin system to fire are explored in Chapter 6. In some pine trees, there is an additional inducible response to bark beetles and pathogens. In this system, damage to phloem tissue triggers the rapid synthesis of phenols, terpenes, and resin acids within the surrounding cells (Reid et al. 1967, Raffa and Smiley 1988, Klepzig et al. 1996). These cells fill with secondary metabolites, die, and present a physical and chemical barrier that can limit intrusion into the surrounding tissue. Relatively little is known about effects of environment, genotype, or tree age on the efficacy of this necrotic defense system in red pines, and it was beyond the scope of this research to explore it. These studies focused on red pine because this species is of central importance to park management. Chapter 1 includes comparisons of resin flow among the three species of pines that occur at Itasca.

Tree defenses interact with beetle abundance to influence tree susceptibility to attack. In general, we expect trees with higher defenses (e.g., higher levels of constitutive resin flow) to be less susceptible to bark beetles. However, even well defended trees can succumb to high rates of attack by bark beetles because as attack rate increases, the constitutive resin can be depleted and the carbohydrate reserves to support inducible responses can be exhausted (Raffa and Berryman 1983). Therefore, the probability of successful attack is expected to increase with increasing attack rate at any level of constitutive resin flow (Fig. 2.2). One result is that high abundance of bark beetles can beget high reproductive success by the beetles, which begets even higher abundance of bark beetles and creates a positive feedback system that can potentially devastate a forest. This scenario was a primary rationale for bark beetle control efforts and bark beetle research at Itasca following the extensive windstorms in 1995-96.

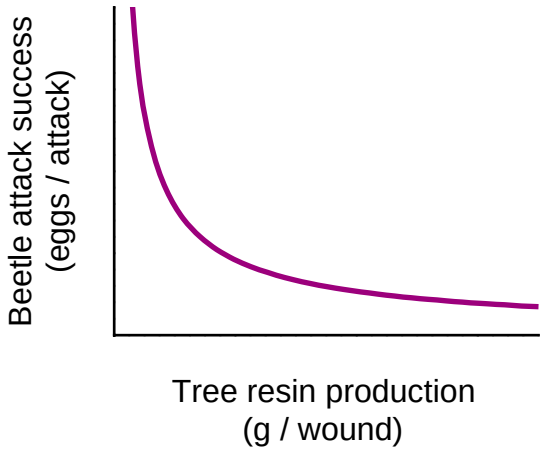

Figure 2.1: Hypothesized relationship between beetle reproductive success and tree resin flow. Beetle reproductive success in this system is thought to be chiefly restricted to trees with very low resin flow (i.e., low secondary metabolism). This particular function has been parameterized with experimental data for the southern pine beetle (Reeve et al. 1995), which is thought to be more tolerant of resin flow than *Ips*.

The physiology of pine trees, and their resistance to bark beetle attack, could be influenced by variation in water availability, nutrient availability, competition with nearby trees, and other environmental effects. If so, there would be predictable patterns in the susceptibility of pines to beetle attack that could be used to assess risks and guide strategies for monitoring and control. There could be important spatial variation in tree defenses among old-growth stands of red pine at Itasca. If so, identifying attributes of those stands could allow for site-specific management strategies. For example, stands with high susceptibility to bark beetles would merit careful monitoring for beetle infestations, could be given special consideration for beetle control efforts (e.g., rapid removal of trees that fall from windstorms or snowstorm), and could be protected against any avoidable risks of exacerbating mortality from beetles (e.g., by minimizing exposure to prescribed burns, see Chapter 6). We evaluated spatial variation in tree growth and defenses against bark beetles with a standardized sampling scheme that included 20 mature red pines within each of 12 old-growth stands scattered throughout the park. Measurements included an assortment of tree and stand characteristics that might be associated with tree defenses and could allow the easy identification of stands that are more or less resistant to bark beetles.

We also evaluated the effects of tree age on growth and defenses. It could be that the old-growth stands of red pine at Itasca are approaching senescence and, as a consequence, have rapidly declining levels of defense against insects and pathogens. If so, tree mortality from beetles might be expected to accelerate over the next two or three decades, in which case appropriate management strategies might be very different than if the forest could realistically persist through another century. For example, if the expected lifetime of the forest is only a few decades, it might be sensible to pursue very aggressive regeneration programs, perhaps involving frequent prescribed burns and plantings, even at the expense of some immediate costs in tree mortality (because the expected future lifespan of the trees would be very short in any case). If, instead, the old trees are still physiologically vigorous and relatively well defended, the value of existing trees would be very high (because they are likely to persist for many decades in the absence of extraordinary disturbance) and management strategies should prioritize survival of the existing trees, even at the expense of some limitations on regeneration rate (because it would not matter very much if regeneration was successful in the next decade rather than this decade). We assessed the effects of age on tree defenses by comparing resin flow in replicated stands of old red pines and young red pines that were growing in comparable environments.

Finally, we compared the anti-herbivore defenses of red pines in Itasca with red pines growing in a region of west-central Wisconsin where precipitation is higher, drought is less severe, and growth rates of red pine are near the maximum for red pines anywhere. Because the forests at Itasca are very near to the western distribution limits of red pine, it could be that Itasca forests are chronically stressed and generally susceptible to insects and pathogens. We tested this hypothesis by comparing the resin flow of replicated stands of similarly aged red pines in Itasca and Dunn County, Wisconsin.

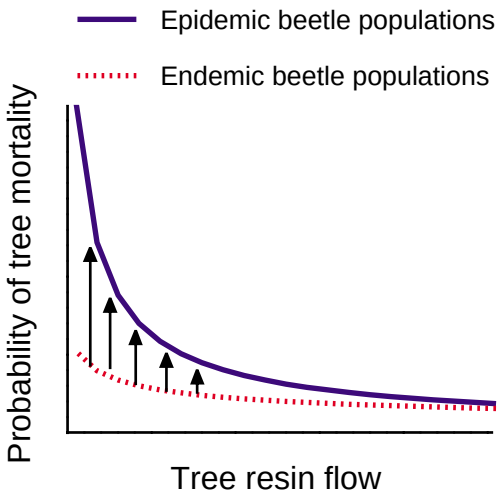

Figure 2.2: The probability of tree mortality from bark beetles is hypothesized to be a function of tree resin flow and bark beetle population size. Upward arrows indicate the potential effects of high population size in bark beetles (epidemic populations) on tree mortality.

2.2 METHODS

We measured variation in resin flow and phloem chemistry within and among 12 stands of old growth red pine in Itasca Park (Fig. 2.3). Resin flow was evaluated by measuring the resin with standardized wounds as described in Chapter 1. Phloem disks were simultaneously collected, dried, and weighed to provide a measure of phloem thickness, which indicates carbohydrate reserves in the tree and is positively related to nutritional suitability for bark beetles in the absence of tree defenses (as in a blowdown). We measured height, diameter, and percent live crown for each tree, and measured the local density of trees around each study tree with an English BAF 10 prism. Two fascicles (dropped the previous year) were collected from the base of each tree to compare needle morphology among sites.

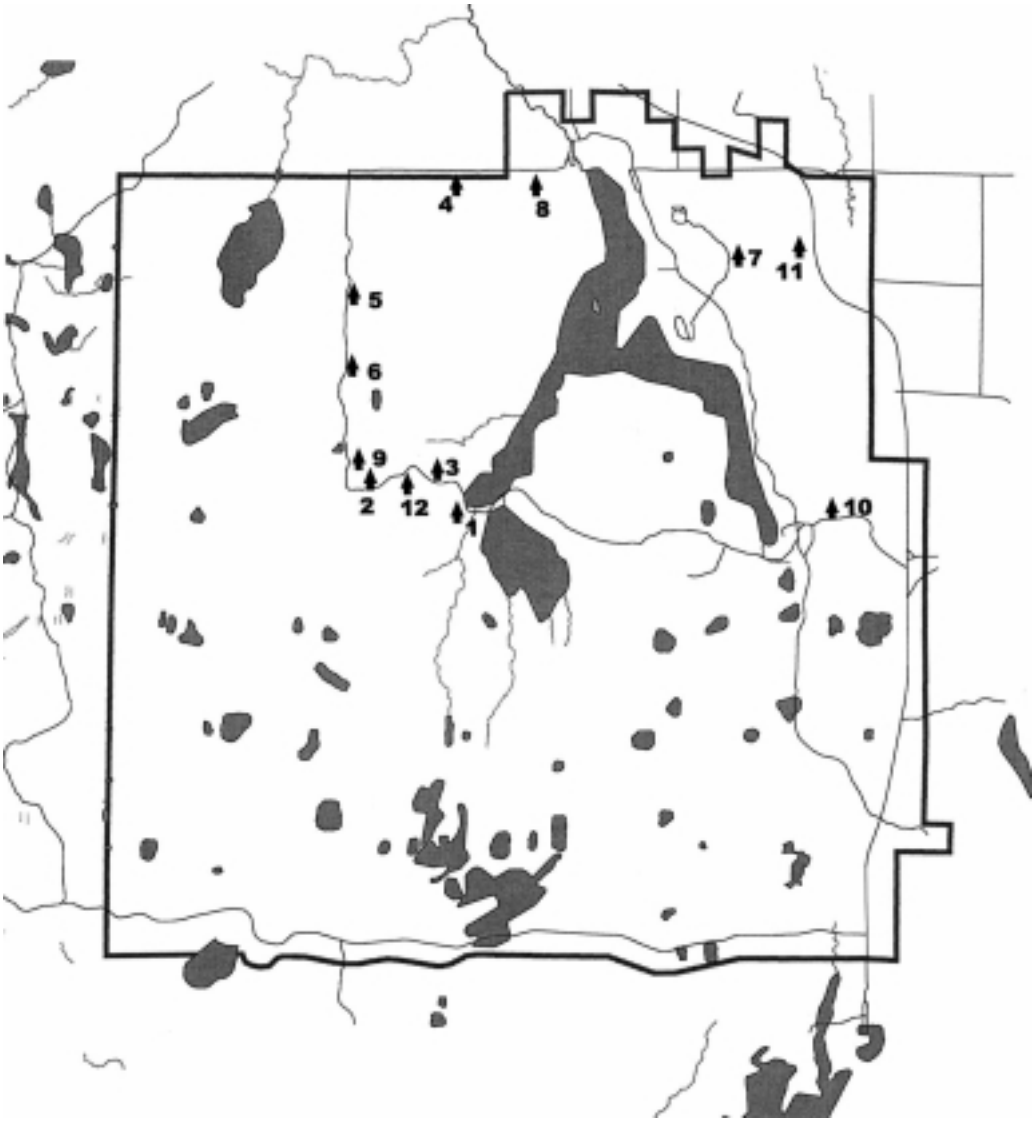

Fig. 2.3. Location of 12 study sites where we measured growth and constitutive resin flow in old growth stands of red pine at Itasca State Park.

We measured the gap light index (GLI) at each site with digital analysis of eight photographic samples collected from each site with a fisheye lens (Fig. 2.4; Canham 1988). Gap light index is inversely related to canopy closure, so provides a measure of competition among tree crowns. Two soil cores (22 mm diameter) were extracted from each stand on 25 August 1997 to measure depth of organic layer and percent water. During 1998, we also compared relative soil moisture at each site using a neutron probe. The elevation of each site was measured with an altimeter calibrated before and after each measuring bout at a site of known elevation (Mississippi headwaters).

One core was extracted from each tree at 1.5 m and subsequently analyzed as described in Chapter 5 to reconstruct the growth histories of the trees. Half of the trees were cored in 1997 using a 6" corer, and the other half of the trees were cored in 1998 with a 10" corer. The 10" corer reached the center of the trees so provided tree age as well as annual growth. For those cores that included the central ring, we estimated the year in which a tree germinated as five years before the age of the core (to allow for growth of the seedling to 1.5 m. For each tree, we extracted six different growth parameters from the ring data to test for physiological correlations between tree defenses (resin flow), age, and growth. *Grow62* = average radial growth for 62 years from 1935 – 1996. *Grow10* = average radial growth for the most recent 10 years. *CVGrow* = the coefficient of variation in annual growth *(*a measure of physiological stability in the tree; = standard deviation in annual growth over 62 years divided by the average annual growth). *Slope* = the slope from a linear regression of annual growth vs. year over the 62 year time series (negative slope indicates declining growth and positive slope indicates increasing growth). *DroughtGrow* = the magnitude of growth decreases during a drought that occurred from 1988-90, defined as annual growth in 1990 (the nadir of the drought) minus the annual growth in 1986 (the zenith of growth prior to the drought). *%Latewood* = the percentage of annual radial growth that was made of latewood rather than earlywood, which is potentially relevant to resin flow in that the majority of vertical resin ducts are formed within the latewood, so trees with relatively more latewood could have relatively more resin ducts.

2.3 Results and discussion

Age and growth of mature red pines. We obtained the age of 71 mature red pines (4-9 trees at each of the 12 sites). Overall, the median year of establishment was 1850 (SD = 36 years). The oldest tree in the sample reached 1.5 m in height in 1770. There was at least one tree dating to the late 1700s at sites 2, 10, and 11. The youngest tree in the sample dated to 1922 and came from site 11, the same site as one of the oldest trees. Among sites, the oldest median age of establishment was in 1819 (site 7) and the youngest median age of establishment as 1902 (site 10). Sites 3, 4, 6, 7, and 8 were even-aged (standard deviation in age of establishment of 3-9 years). Sites 1, 2, 9 and 12 contained trees of mixed ages (SD in age of establishment of 15-25 years). Sites 10 and 11 were of very uneven ages (SD in age of establishment of 46 and 59 years). The fact that half of the sites were of mixed age indicates that stand-clearing fires have not always been required for the regeneration of red pine at Itasca. At these sites, we found adjacent trees that differed in age by as much as 50 - 140 years. The even ages at sites 3, 6, and 7, suggest stand-clearing fires at those sites in approximately 1830, 1826, and 1811 respectively. Sites 4 and 8, which are near each other in the north end of the park, were both established in about 1888-89, presumably as a result of the same stand-clearing fire.

Our estimates of stand ages at Itasca must be qualified because the sample of trees that we were able to age may be biased towards younger trees. In 1998, we used a 10" corer to extract cores from 110 trees (those with ID numbers from 1001 - 1120 in Appendix 2, excepting site 5). These 110 trees were a representative sample of the tree population, but the core missed the center of the tree (and therefore did not provide the age) in 39 cases. The trees for which we lack ages tended to be of larger diameter than the trees we were able to age (least square means ± SE = 49.1 ± 1.7 cm vs. 39.1 ± 1.1 cm) and so may have tended to be older. This probably did not affect our estimates of age within the five stands that were clearly even-aged, but we may have underestimated the median age in stands 1, 2, 9, and 12 where we were unable to age 17 of 40 trees. In retrospect, this potential bias was unfortunate but does not affect any of the central conclusions in this report.

For images see
http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm

Fig. 2.4. Representative canopy photographs used to compare the extent of canopy closure within and among stands of mature red pine at Itasca. Images were collected with an 8 mm fish-eye lens and digitally analyzed (Canham 1988). Upper image, taken near tree 68 at site 7, yielded a gap light index of 54%. Lower image, taken near tree 52 at site 6, yielded a gap light index of 32%.

Appendix 1 shows the pattern of annual growth from 1935 to 1996 for each of 20 individual trees at 12 sites. Radial growth per year ranged from highs near 4 mm to lows of less than 0.3 mm. Trees with intermediate crown classes tended to grow slower than trees with codominant crown classes. This relationship can potentially reflect both cause and effect in that slow-growing trees are less likely to attain codominant crown stature and trees that do not share the upper forest crown are less likely to attain high radial growth. There was considerable variation among trees in the temporal patterns of growth. For example, tree 1077 in site 8, has increased its annual growth from less than 0.4 mm in the late 1940s to > 2 mm per year since 1972. Presumably, this reflects the death of one or more nearby trees. In contrast, tree 82 in site 9 has declined from near 2 mm / year in the late 1930s to near 0.6 mm / year in the last two decades. Trees 1073 and 1075 in site 8 have been sustaining high growth rates near 2 mm / year throughout the last 60 years, while other trees, such as tree 1102 in site 11, have been barely growing through the entire time series (average = 0.33 mm / year).

Overall, there was only a weak tendency for declining growth rates during this century in the population of mature red pines at Itasca (Fig. 2.5, upper). Average radial growth rates held near 1 mm / year for most of the time series, with distinct peaks in 1942 and 1952, and conspicuous troughs from about 1978-82 and from 1989-91. The latter trough corresponds to a sequence of drought years (minimum Palmer drought severity index = -6, -4, and -5). Other patterns in the time series are not easily explained by the Palmer drought severity index, but climatic conditions, perhaps related to temperatures or length of the growing season, are the most likely mechanism for synchronous effects on forest growth. When the aged trees were pooled across sites, there was some tendency for older trees to have lower growth rates (*Grow62* in Fig. 2.6), but there were no effects of age on physiological stability as measured by interannual variation in growth rate (*CVGrow* in Fig. 2.6), nor were old trees any more likely to be in growth decline than young trees (*SlopeGrow* in Fig. 2.6). Furthermore, older

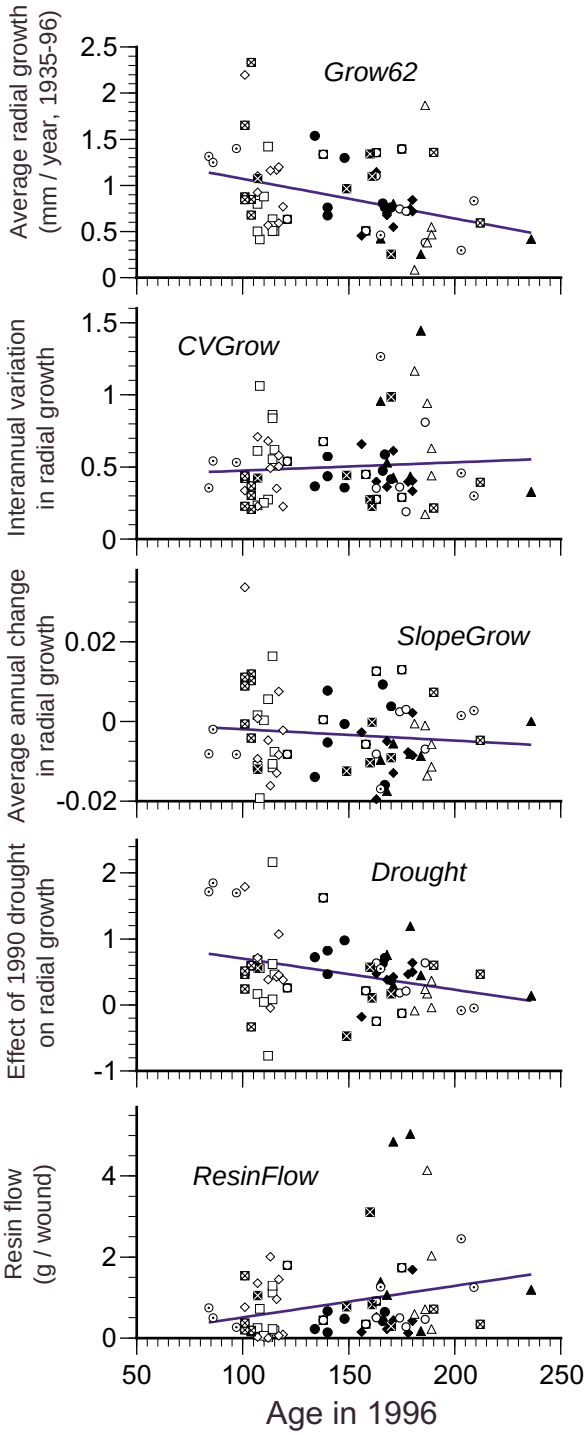

Fig. 2.6. Correlations of tree age with four different measures of tree growth and with constitutive defense against bark beetles (resin flow). Different symbols represent different sites.

trees actually tended to suffer less impacts from the most recent drought (*DroughGrow* in Fig. 2.6), and tended to have significantly higher constitutive resin flow than younger trees (*ResinFlow* in Fig. 2.6). These data indicate generally high vigor and high defense in even the oldest red pines at Itasca. There is no suggestion of physiological senescence or growth declines in trees up to almost 250 years old. In the absence of mortality from windstorms, bark beetles, fires, lightning, icestorms, and other disturbances, it seems realistic to expect that many mature red pines in Itasca could live for another century or more. This argues for placing a high priority on minimizing any manageable risks of tree mortality from disturbance. Given the long potential lifespan of these trees, even very small increases in mortality risk can have a meaningful effect on tree survivorship and the lifetime of the forest (see Figs. 5.7 and 6.9 in Chapters 5 and 6)

Variation in growth and defenses among old growth red pine. There was highly significant variation among old growth stands of red pine in constitutive resin flow and all measurements of tree growth, tree morphology, and stand attributes (Figs. 2.7 - 2.9; $F_{11, 201} = 12.39$, $P < 0.0001$ for site effect for resin flow). Measurements of resin flow were quite consistent between measurements in August 1997, July 1998, and August 1998 (Fig. 2.12; highly

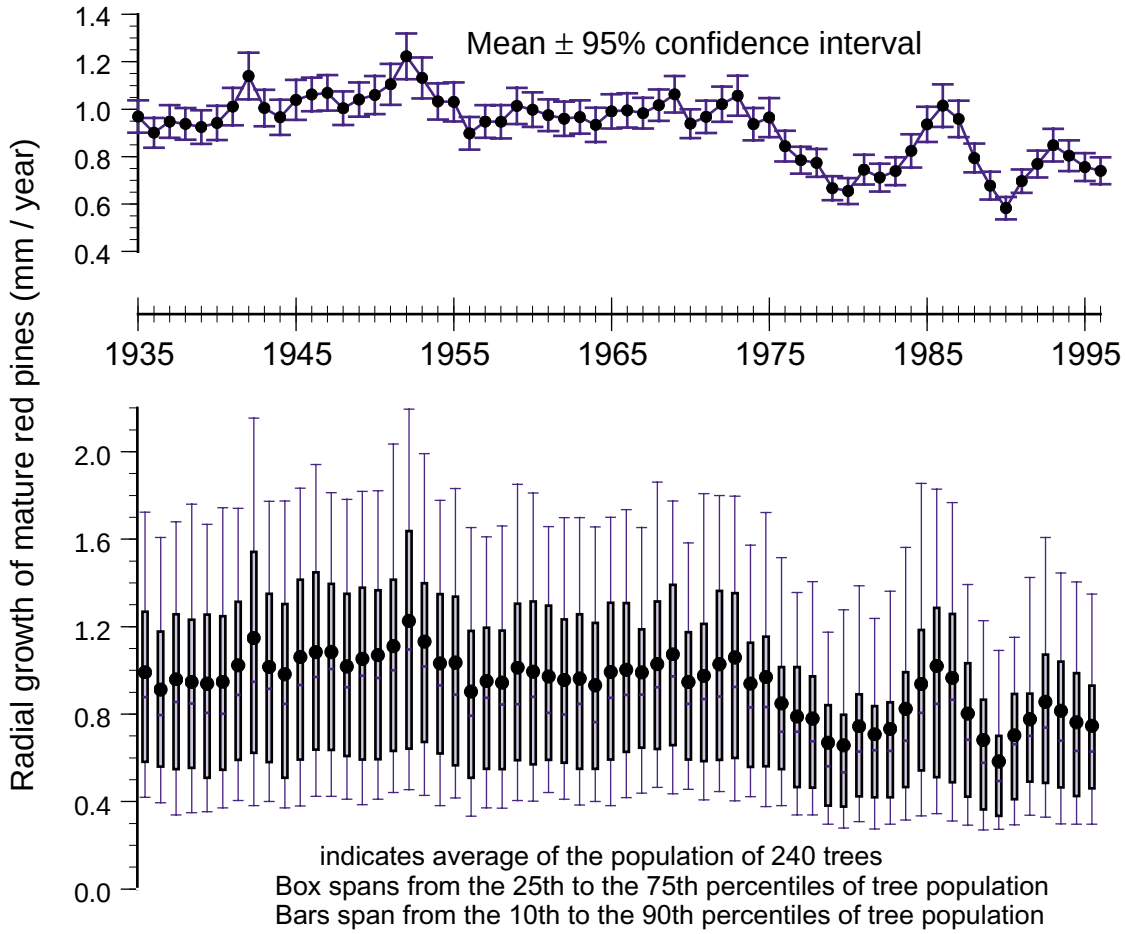

Fig. 2.5. Annual growth of mature red pine at Itasca during 1935 - 1996. Upper figure shows population mean with confidence interval. Lower figure summarizes the frequency distribution of the population (20 trees at each of 12 sites). Trough in growth rates from 1988 - 1990 correspond to a significant drought in the region.

significant effects of tree: $F_{201, 198} = 4.41$, $P < 0.0001$; no effects of data: $F_{1, 198} = 0.01$, $P = 0.93$ for comparisons of 240 trees across two dates in 1998, and $F_{2, 166} = 2.00$, $P = 0.10$ for comparisons of 120 trees that were measured on all three dates). Patterns of resin flow across sites remained very constant across the 3 sampling dates ($r = 0.78$ to 0.89 for correlations of sites means across dates). Patterns of phloem thickness were equally similar across sampling dates. Thus the old growth forest at Itasca is comprised of a mosaic of red pine stands that differ in their constitutive defenses against bark beetles and many other attributes as well.

We explored correlations among site-specific characteristics (Tables 2.1 - 2.2; Fig. 2.10) and used stepwise regression to identify the simplest combinations of parameters that could predict spatial patterns in constitutive resin flow. Tree diameter had a strong positive relationship with average resin flow at a site (Fig. 2.10). Equation 2.1 explained 63% of the variation among sites in resin flow ($P = 0.0019$ for the statistical effect of diameter, *DBH*). There appeared to be some additional contribution of basal area once the effects of diameter had been accounted for. A model that also included basal area (Eq. 2.2) explained 74% of the variation among sites in resin flow ($P = 0.0021$ and $P = 0.082$ for effects of *DBH* and *BA*, respectively). The coefficients for diameter were positive, indicating that sites with bigger trees tended to have higher resin flow. The coefficient for basal area was negative, indicating that if average tree diameter is comparable, sites with high basal area tended to have lower resin flow than sites with high basal area. Differences among sites in average tree diameter appear to be largely influenced by stand age ($r = 0.65$ for correlation between stand age and DBH), so equations 2.1 - 2.2 reflect the same pattern as indicated in Fig. 2.6 lower. Comparisons of resin flow in mature red pine vs those 30 - 80 years old further reinforce the conclusion that the constitutive resin flow of red pines tends to increase markedly with age (see next section). Presumably, the negative effect of basal area on resin flow is because increased competition among trees for canopy space within a stand tends to limit the carbon resources that are available for the synthesis of oleoresin.

$$Resin = -0.51 + 0.034 \cdot DBH \qquad \textbf{Eq. 2.1}$$

$$Resin = 0.00 + 0.031 \cdot DBH - 0.013 \cdot BA \qquad \textbf{Eq. 2.2}$$

There were numerous other correlations among stand attributes (Table 2.2, Fig. 2.10). Most of these are obvious. For example, tree height was positively correlated with diameter and stands with low basal area tended to have open canopies (high gap light index). Other relationships would have been less easy to predict. The extent of canopy closure changed systematically over an elevation gradient of only 50 m, with higher sites tending to have more open canopies (higher gap light index); the tallest trees tended to occur on the sites where the water content of the organic soil was highest (in September 1997); the greatest effects of a recent drought (1988-1990) were most evident in sites where the water content of the mineral soil was lowest (in September 1997); and sites where trees had the lowest interannual variation in radial growth (*CVGrow*) were the sites most likely to have declining growth rates (Fig. 2.10).

In addition to variation among sites, there were strong differences within sites between trees that were classified *a priori* as belonging to codominant or intermediate crown classes (resin flow averaged 43% higher, and phloem mass 11% higher in codominant vs intermediate trees; $F_{1, 201} = 80.39$ and 30.11, respectively; $P < 0.0001$ in both cases). Trees of intermediate crown class were significantly shorter, of smaller diameter, and their wood tended to be comprised of a higher percentage of latewood (Figs. 2.7 - 2.8; $P < .01$ for all parameters; the result that intermediate trees had relatively more latewood but lower resin flow was opposite the prediction based on density of vertical resin ducts.) However, trees of intermediate crown class did not have relatively less live crown (*%LiveCrown*), did not have conspicuously lower rates of radial growth (*Grow62* and *Grow10*), were no more likely to have declining growth rates (*Slope*), and were no more susceptible to growth reductions from drought (*Drought*) or other climatic factors that influence year-to-year variation in growth rates *(CVGrow*) (Figs. 2.7 - 2.8).

The full set of measurements summarized in this section are provided in Appendix 2. Neutron probe measurements of soil water, which were collected in September 1998, are provided in Appendix 3.

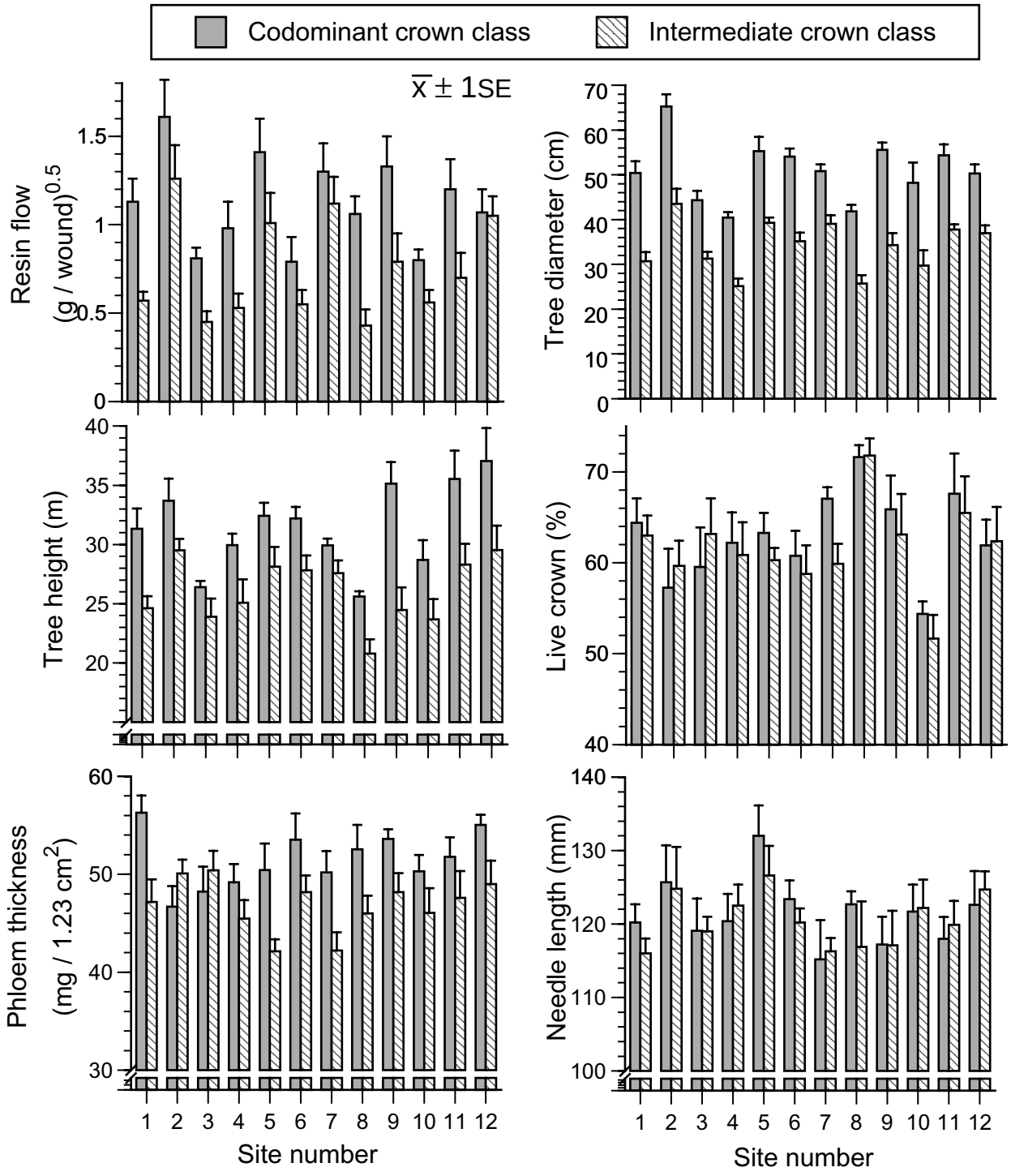

Fig. 2.7. Average characteristics of mature red pines at each of 12 different sites in Itasca Park. *N* = 10 codominant trees and 10 intermediate trees at each site. Analysis of variance indicated significant variation among sites for all parameters.

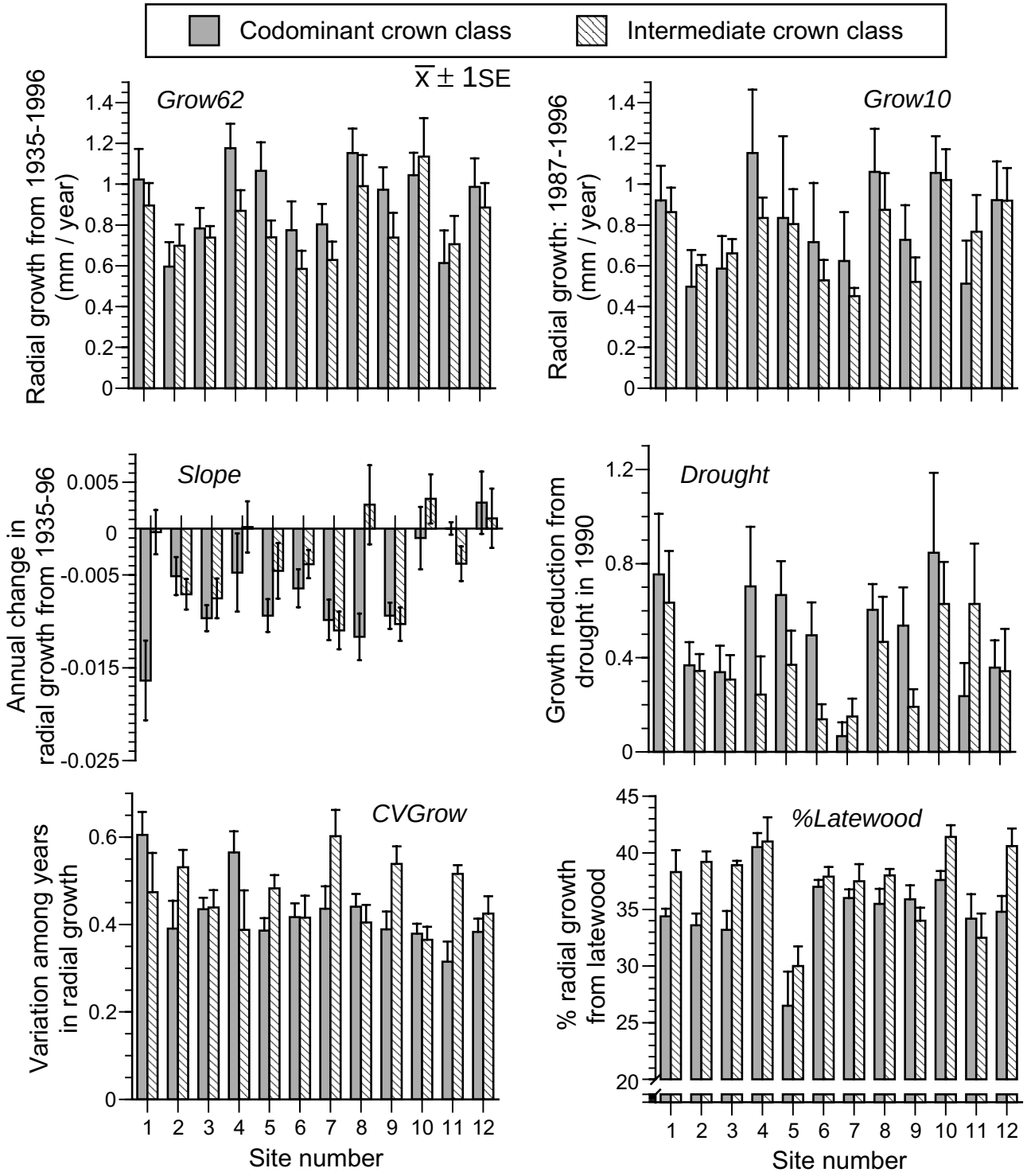

Fig. 2.8. Average characteristics from analysis of tree cores of mature red pines at each of 12 different sites in Itasca Park. *N* = 10 codominant trees and 10 intermediate trees at each site. Analysis of variance indicated significant variation among sites for all parameters.

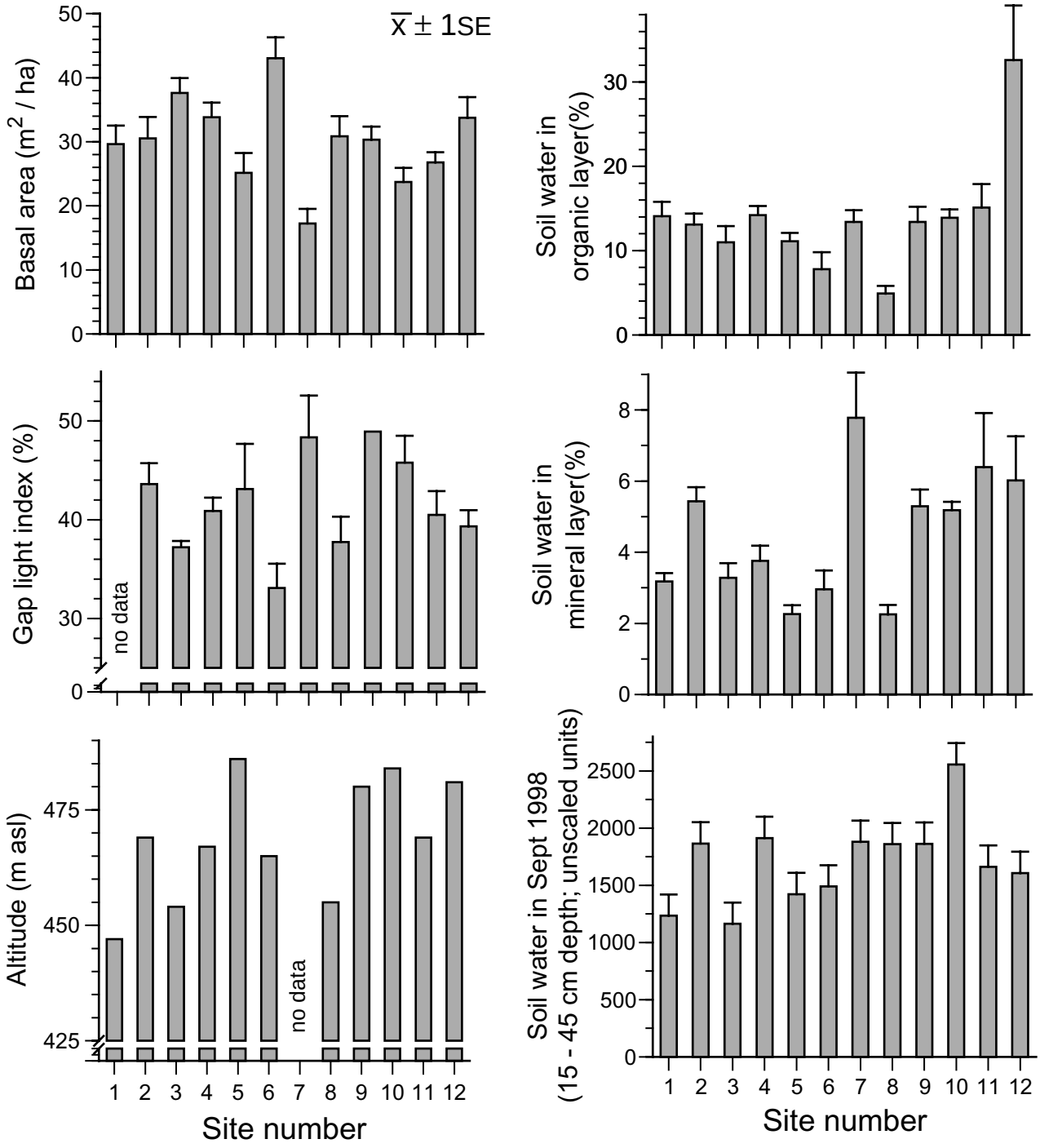

Fig. 2.9. Average site characteristics in each of 12 stands of mature red pine in Itasca Park. Analysis of variance indicated significant variation among sites for all parameters.

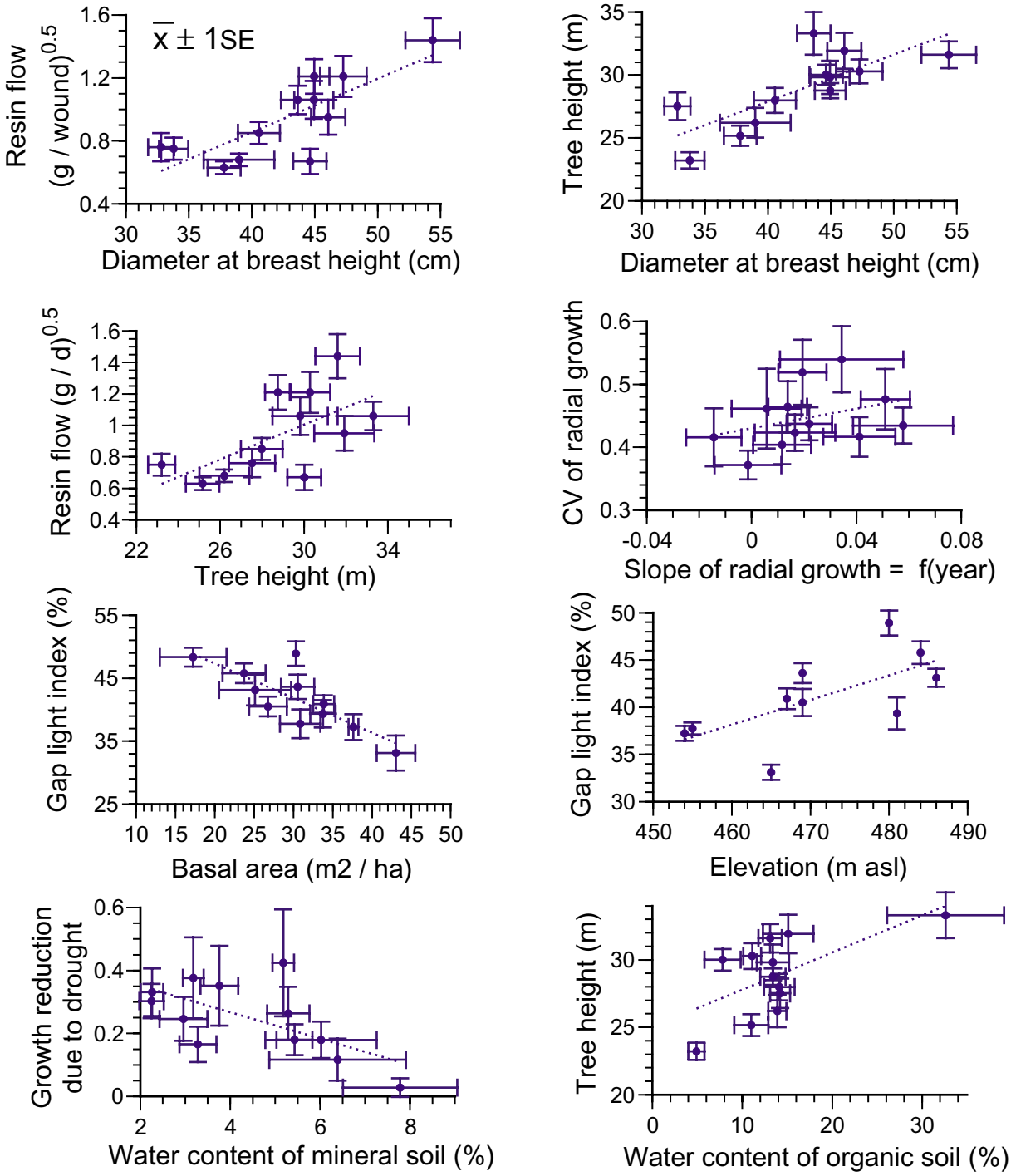

Fig. 2.10. Some of the significant correlations among sites in the attributes of mature red pine stands. See Tables 2.1 - 2.2 for site specific means and correlation matrix.

Table 2.1. Mean attributes of 12 old growth red pine sites in Lake Itasca Park (20 trees / site; see Appendix 2 for measurements of individual trees).

Site	*Age*	*Elev.*	*GLI*	*DepthOrg*	*WaterOrg*	*WaterMin*	*WaterN*	*DBH*	*BA*	*Ht*	*%LC*	*Resin*	*Phloem*	*Fasc*	*Grow62*	*Grow10*	*CVGrow*	*Slope*	*Drought*	*Latewood*
1	148	447		29.7	14.1	3.2	1234	40.6	29.6	28.0	63.7	0.85	51.7	118.1	0.96	0.89	0.54	-0.0084	0.38	36.4
2	175	469	43.6	30.7	13.1	5.4	1866	54.4	30.5	31.6	58.5	1.44	48.4	125.2	0.65	0.55	0.46	-0.0061	0.18	36.4
3	171	454	37.2	25.6	11.0	3.3	1163	37.8	37.6	25.2	61.4	0.63	49.3	119.1	0.76	0.62	0.44	-0.0086	0.17	36.0
4	112	467	40.9	28.7	14.2	3.8	1913	32.8	33.8	27.5	61.5	0.76	47.3	121.5	1.02	0.99	0.48	-0.0023	0.35	40.8
5		486	43.1	27.7	11.1	2.3	1423	47.3	25.1	30.3	61.8	1.21	46.3	129.3	0.90	0.82	0.43	-0.0070	0.33	28.3
6	176	465	33.1	26.4	7.8	3.0	1490	44.6	43.0	30.0	59.8	0.67	50.9	121.8	0.68	0.62	0.42	-0.0051	0.25	37.5
7	187		48.3	26.4	13.4	7.8	1880	45.0	17.2	28.8	63.5	1.21	46.2	115.8	0.72	0.54	0.52	-0.0104	0.03	36.8
8	113	455	37.7	26.4	4.9	2.3	1860	33.8	30.9	23.2	71.7	0.75	49.3	119.8	1.07	0.97	0.42	-0.0045	0.30	36.8
9	161	480	48.9	31.2	13.4	5.3	1863	44.9	30.3	29.8	64.5	1.06	50.9	117.2	0.86	0.62	0.46	-0.0098	0.26	34.9
10	104	484	45.8	31.2	13.9	5.2	2557	39.0	23.7	26.2	53.0	0.68	48.2	122.0	1.09	1.04	0.37	0.0011	0.42	39.5
11	131	469	40.5	29.1	15.1	6.4	1662	46.1	26.8	31.9	66.5	0.95	49.7	119.0	0.66	0.64	0.42	-0.0019	0.12	33.4
12	158	481	39.3	27.3	32.6	6.0	1608	43.6	33.7	33.3	62.1	1.06	52.0	123.7	0.94	0.92	0.40	0.0020	0.18	37.7

Table 2.2. Correlation matrix of site-specific attributes. Significant correlations are in bold.

	Age	*Elev.*	*GLI*	*DepthOrg*	*WaterOrg*	*WaterMin*	*WaterN*	*DBH*	*BA*	*Ht*	*%LC*	*Resin*	*Phloem*	*Fasc*	*Mean60*	*Mean10*	*CVGrow*	*Slope*	*Drought*	*Latewood*
Age	1.00																			
Elev.	-0.10	1.00																		
GLI	0.03	**0.66**	1.00																	
DepthOrg	-0.31	0.36	**0.60**	1.00																
WaterOrg	0.09	0.38	0.12	0.13	1.00															
WaterMin	0.30	0.42	0.58	0.25	0.51	1.00														
Neutron	-0.50	0.50	0.55	0.51	0.00	0.40	1.00													
DBH	**0.65**	0.39	0.28	0.28	0.17	0.41	-0.09	1.00												
BA	0.13	-0.41	**-0.80**	-0.28	-0.05	-0.52	-0.44	-0.19	1.00											
Ht	0.43	0.49	0.12	0.24	**0.62**	0.48	-0.13	**0.77**	-0.01	1.00										
%LC	-0.06	-0.43	-0.16	-0.36	-0.19	-0.14	-0.34	-0.23	-0.02	-0.17	1.00									
Resin	0.50	0.42	0.55	0.26	0.27	0.47	0.03	**0.80**	-0.48	**0.64**	0.01	1.00								
Phloem	0.11	-0.31	-0.42	0.11	0.36	-0.08	-0.34	-0.02	0.56	0.21	0.18	-0.27	1.00							
Fasc	-0.13	0.55	-0.20	0.05	0.13	-0.36	-0.02	0.33	0.13	0.33	-0.37	0.31	-0.25	1.00						
Grow62	**-0.76**	0.07	0.08	0.16	0.07	-0.38	0.36	**-0.71**	-0.11	-0.52	0.02	-0.40	0.00	0.09	1.00					
Grow10	**-0.83**	0.07	-0.12	0.14	0.18	-0.38	0.31	**-0.67**	-0.01	-0.37	-0.05	-0.44	0.05	0.24	**0.94**	1.00				
CVGrow	0.38	-0.55	0.42	0.02	-0.12	0.09	-0.34	0.05	-0.24	-0.03	0.26	0.30	-0.09	-0.42	-0.15	-0.27	1.00			
Slope	**-0.61**	0.39	-0.29	0.15	0.51	0.11	0.43	-0.21	0.12	0.18	-0.27	-0.25	0.17	0.36	0.39	**0.62**	**-0.70**	1.00		
Drought	**-0.68**	0.07	-0.04	0.41	-0.20	**-0.64**	0.22	-0.44	0.14	-0.39	-0.26	-0.42	0.07	0.31	**0.77**	**0.77**	-0.15	0.26	1.00	
Latewood	-0.39	-0.25	-0.12	0.07	0.15	0.19	0.44	-0.49	0.25	-0.29	-0.27	-0.44	0.18	-0.37	0.29	0.32	0.00	0.37	0.14	1.00

Age = median age in 1996. *Elev* . = m above sea level. *GLI* = gap light index (% light transmission through canopy). *DepthOrg* = depth of organic layer (cm).
WaterOrg = water content of organic layer in September 1997 (% mass). *WaterMin* = water content of upper mineral layer in September 1997 (% mass).
WaterN = soil water content in August 1998 as measured by neutron probe (unscaled units). *DBH* = diameter at breast height (cm). *BA* = basal area (m2 / ha).
Ht = tree height (m). *%LC* = percent live crown (% of total height). *Resin* = resin flow / wound (square root transformed). *Phloem* = phloem thickness (mg dry mass / 1.23 cm2).
Fasc = fascicle length (mm). G*row62* = average radial growth for 62 years from 1935 to 1996 (mm / year). G*row10* = average radial growth for 10 years from 1987 to 1996.
CVGrow = coefficient of interannual variation in annual radial growth (SD / mean). *Slope* = slope from linear regression of annual radial growth vs year from 1935 to 1996.
Drought = reduction in annual radial growth due to drought: growth in 1986 (predrought) - growth in 1990 (drought).
Latewood = percent of radial growth comprised of latewood xylem vs earlywood xylem.

Constitutive defenses of mature red pine vs. young red pine. Mature red pines at Itasca had dramatically higher resin flow (about two-fold) compared to red pines in the same area that were 35 - 60 years old (Fig. 2.11 - 2.12). It could be that old trees have higher resin flow as a result of physiological changes associated with maturation, such as an increase in the size and integration of the resin duct system. It could also be the result of tree responses to wounds that tend to be accumulated during the lifespan of a long-lived tree (i.e., if wounds from insects, fires, pathogens, and mechanical damage induce incremental, sustained, increases in resin flow). It is also possible, but perhaps less likely, that old growth forests represent a subset of the original tree population that has been selected for those individuals that are best defended against bark beetles. In any case, these results strongly reinforce the conclusions from growth analyses that mature red pines at Itasca are not senescing and are not poorly defended against bark beetles. This conclusion is consistent with our observations in charred trees that came under beetle attack of strong resinous barriers around the site of the attack that limited the extent of permanent damage to the cambium. In fact, our results indicate that they should be generally more resistant to bark beetles, and suggest that mortality from bark beetles (Chapter 5) is the product of long exposure to low risks rather than an indication of a forest that is in rapid decline.

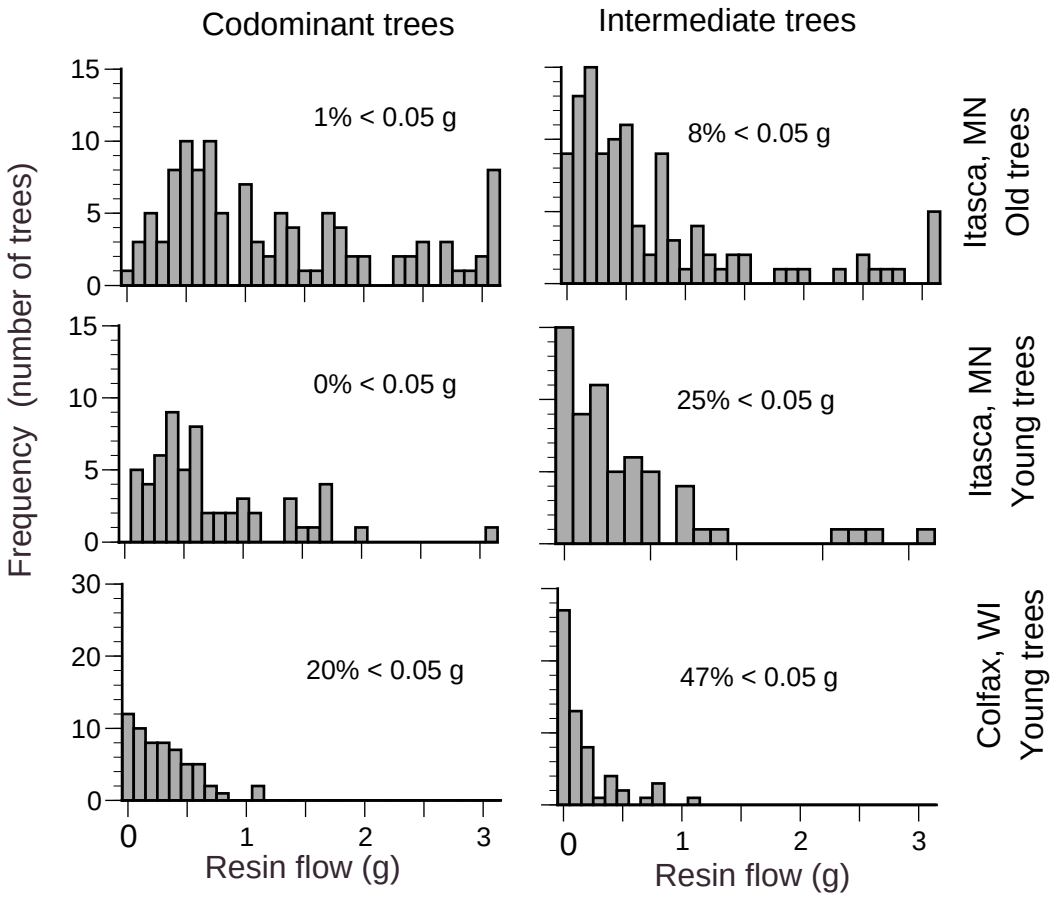

Fig. 2.11. Frequency distribution of resin flow, a measure of tree defenses against bark beetles, for mature red pines at Itasca (≈100 - 250 years old), younger red pines at Itasca (30 - 78 years old), and young red pines near Colfax, Wisconsin (31 - 40 years old). Average resin flow differed between the populations, as did the proportion of trees that lacked constitutive resin defenses against bark beetles. In old trees at Itasca, < 10% of the trees lacked resin flow, compared to up to 25% of the young trees at Itasca, and up to 47% of the young trees in west central Wisconsin.

Constitutive defenses of red pine at Itasca compared to more favorable sites in Wisconsin. For comparably aged red pines, resin flow averaged nearly twice as high in Itasca compared to WI (Figure 2.11 - 2.12). In Itasca, none of the young codominant trees, and only 25% of the young intermediate trees had zero resin flow, compared to 20% of the young codominant trees and 47% of the young intermediate trees in WI (compare middle and bottom pairs of histograms in Fig. 2.11). These results are exactly contrary to the hypothesis that trees growing on marginal sites, such as Itasca, will tend to be less well defended against bark beetles, than trees growing on high quality sites. The site index for young stands at Itasca ranged from 50 to 69 feet (site index = expected height at 50 years), substantially lower than the site indexes of 71 to 83 feet at sites in west central Wisconsin. Across sites there was a significant negative correlation between resin flow and site index (Fig. 2.13).

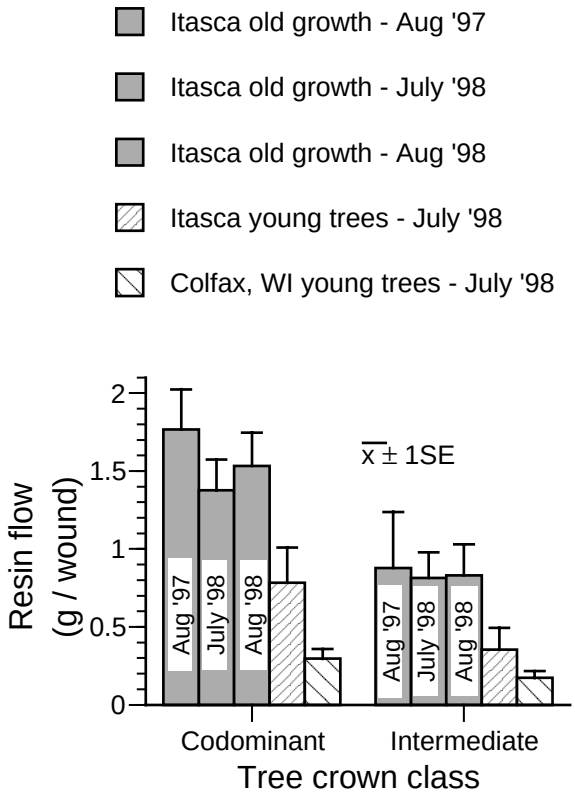

Fig. 2.12. Average resin flow in mature red pines at Itasca, young red pines at Itasca, and young red pines in west central Wisconsin. Differences among tree populations was highly significant.

This result seems counter-intuitive if it is assumed that trees under all environmental conditions invest an equal proportion of their carbon resources into resin production. However, it is completely consistent with an alternative physiological model (Lorio 1986, Reeve et al. 1985, Wilkens et al. 1997), which recognizes that the carbon available for secondary metabolism (e.g., resin synthesis) often depends upon the carbon resources that are left after investments to growth. Tree growth is frequently limited by water and nutrient availability more than it is limited by carbon. Site indexes for red pine are largely a function of water and nutrient availability. Growth potential of red pine at Itasca is low in large part

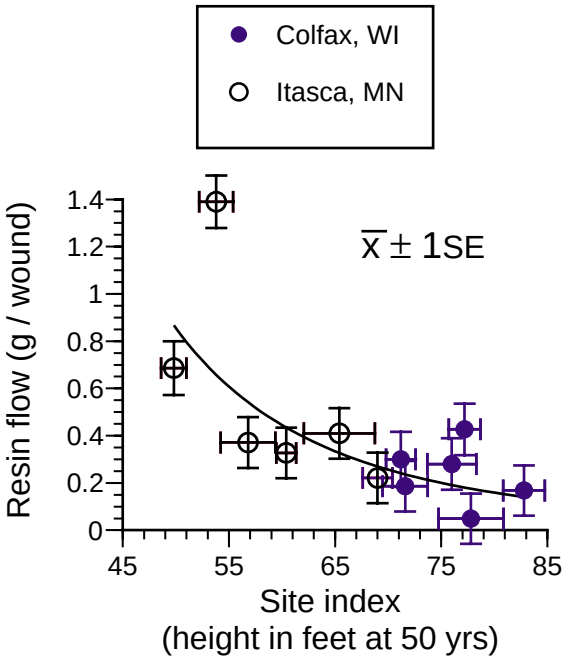

Fig. 2.13. Relationship between resin flow and site index for 30-80 year old red pines at Itasca and in west central Wisconsin. Red pines grow relatively slowly near Itasca (expected height at 50 years of only 49 - 69 feet), but they have higher levels of constitutive defenses against bark beetles. This pattern matches a physiological model that predicts secondary metabolism (resin flow) based upon the carbon resources that are left after trees have grown to the limits set by availability of water and nutrients (Fig. 2.14).

because of water limitations. Moderate water deficits tend to constrain growth more than photosynthesis (Fig. 2.14). Under these conditions, relatively more carbon is left after growth has been maximized to the limits of water availability. If a constant proportion of this carbon remainder goes into secondary metabolism, then resin flow will tend to be highest on sites with moderate water deficiencies and relatively low growth (Fig. 2.14). The comparisons of resin flow in red pines in Wisconsin and Itasca are consistent with this model.

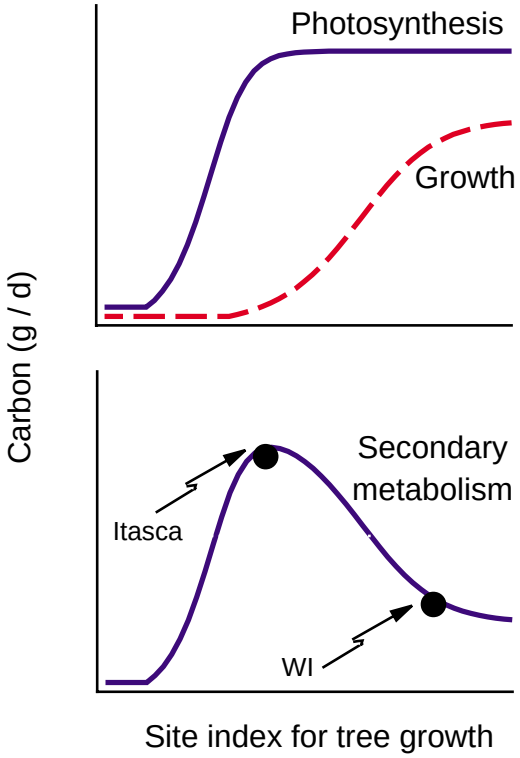

Figure 2.14: Hypothesized relationship between site index for tree growth, which is primarily a function of water and nutrient availability, and patterns of carbon acquisition, growth and secondary metabolism in pine trees (after Lorio 1986, Reeve et al. 1995). At moderate water deficiencies, resin flow and resistance to bark beetles is predicted to be high because tree growth is limited relative to photosynthesis, so there is a larger surplus of carbon for secondary metabolism after growth has been maximized. This model is consistent with the high resin flow of trees at Itasca compared to similarly aged forests in west central Wisconsin, where growth conditions for pine are better (see Fig. 2.13).

In any case, these data strongly falsify the hypothesis that red pines at Itasca are more susceptible to bark beetles because low growth rates are associated with chronic stress and low defenses.

One additional consequence of the interpretation represented in Fig. 2.14 is that drought, which is predicted to increase secondary metabolism and resin flow (i.e., shift trees to the left in Fig. 5), will have opposite effects on resin flow in Itasca and WI, tending to reduce resin flow in Itasca and increase resin flow in WI. This would be consistent with the observations of foresters and forest entomologists which associate drought with pine tree mortality in western MN but not in WI. Our study did not include a period of significant drought, so we can only guess at the magnitude of drought that would be required to compromise tree defenses at Itasca and significantly increase the risk of bark beetle infestations: it might require drought such as only occurs once a century or it might be facilitated by more moderate droughts that occur many times a century. However, the available data clearly indicate that (1) red pine in Itasca are not chronically susceptible to bark beetles compared to red pine in WI and (2) old red pine stands in Itasca are not chronically susceptible to bark beetles because of reduced resin flow associated with senescence and a collapse of the resin duct system. The low growth of red pines at Itasca appears to reduce risks from bark beetles, and therefore increase the potential longevity of the forest.

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Chapter 3
Bark beetle communities at Itasca State Park

3.1 INTRODUCTION

In 1994-96, the old growth pine forests in Itasca State Park sustained a sequence of heavy blowdowns from windstorms. Pine trees blowdowns provide a high quality food resource (fresh, undefended phloem) for *Ips* bark beetles and can permit rapid growth of bark beetle populations. With suitable food resources, *Ips* populations can increase by up to 10-fold per generation or 1000-fold per summer with 3 generations, and a single large pine tree might produce 80,000 beetles (Chapter 1). High populations of *Ips* following blowdowns or other disturbances that increase food resources might promote subsequent attacks in otherwise undamaged trees and lead to significant additional mortality of pine trees as a secondary effect of the blowdowns. It is not known which of the three *Ips* species that inhabit Itasca State Park are most likely to respond to blowdowns with population increases. Nor is it known how long such population increases are likely to persist or whether the population responses tend to be local or regional. These questions are of obvious importance in assessing the spatial scale and temporal duration of risks from windstorms to old growth pine trees at Itasca State Park. In this component of the research, we conducted replicated quantitative sampling of the bark beetle community within and outside of the blowdown area to address these questions.

As part of this research, we also assessed the spatial and temporal responses of bark beetle predators to the resource pulses that result from windstorms. Natural enemies can be potent forces in limiting the abundance of forest insects to levels below that of significant economic or ecological damage. Similarly, competitors can also function to limit the abundance of particular species. This would have special relevance if different species of bark beetles are more or less likely to attack live trees. For example, if *Ips grandicollis* and *Ips perroti* are less likely to attack live trees than *Ips pini*, then increases in the former, less aggressive, species can be viewed as a natural control on the abundance of the more dangerous *I. pini*. Management strategies that incorporate these natural control agents can be cost- effective as well as environmentally friendly. However, this approach requires an understanding of the structure and function of bark beetle communities in Itasca State Park. Consequently, our sampling was also designed to address the following questions. Under baseline conditions (in the absence of blowdowns), what is the relative abundance of *Ips* bark beetles and their natural enemies? What is the relative abundance of the three *Ips* species that occur in the park (*I. pini*, *I. grandicollis*, and *I. perroti*)? What is the seasonal timing of their flight activity and reproduction? How does the abundance and species composition of the bark beetle community change in the presence of blowdowns? Which of the bark beetle species is the most likely to cause tree mortality and which of the natural enemies exerts the strongest control over that species of *Ips*? An additional objective was to assess the efficacy of different pheromones in sampling the various members of the bark beetle community at Itasca State Park.

3.2 METHODS

We used funnel traps and pheromone lures to sample the bark beetle community in 26 pine stands within and around Itasca State Park (Fig. 3.1: 11 sites within undisturbed old growth red pine forest, 5 sites within red pine blowdowns from the storms of 1996, 5 sites in old growth forest near the blowdowns (200 - 300 m distant), and 4 sites in red pine plantations just outside the park (30 - 60 years of age, 1 - 15 km from the park). Each site was sampled with an array of 3 traps separated by 15 m (usually configured as an equilateral triangle); within a site, each trap was baited with either ipsdienol + lanierone (produced and preferred by *I. pini*), ipsenol (produced and preferred by *I. grandicollis*), or ispdienol + ipsenol (produced and preferred by *I. perroti*). Ipsdienol and ipsenol lures had an elution rate of 0.2 mg / d. Traps were implemented by 1 July 1997 and emptied every two weeks through the remainder of the flight season during 1997 (late September). During 1998, trapping was conducted with the same protocol at the same sites from the beginning of flight (early May) until the end of beetle flight (mid-September). Pheromone lures were rotated each time the traps were checked to control against spurious effects of trap position. We counted and identified all *Ips* and *Ips* predators that were captured.

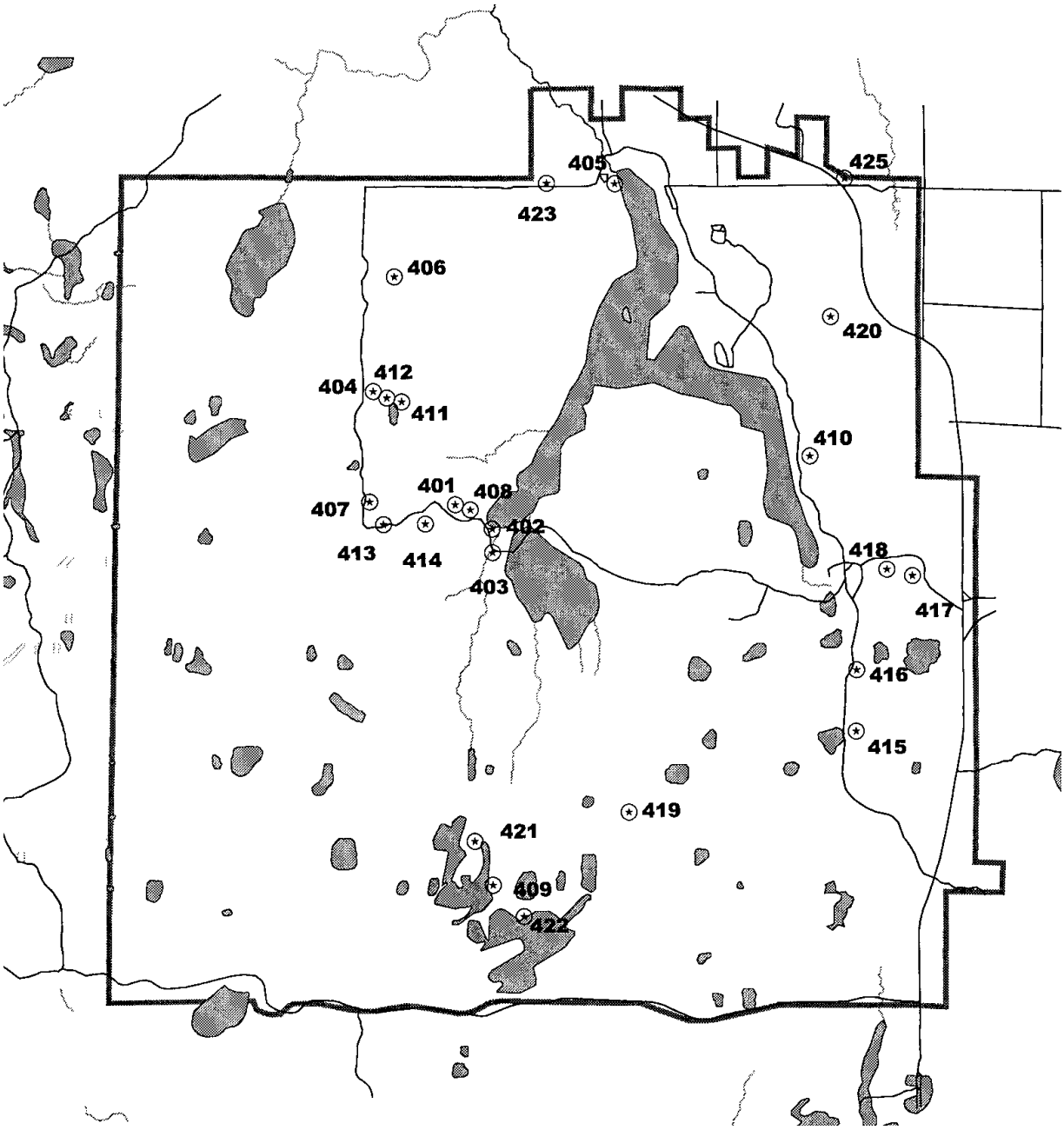

Fig. 3.1. Location of pheromone trap arrays for studies of the responses of *Ips* communities to windstorm disturbance. Appendix 4 indicates the forest type and disturbance class of each stand and provides the full record of beetle captures .

3.3 Results and Discussion

During 1997, 1-2 years after windstorms, the abundance of *I. pini* was 4-5 times higher in the windthrow areas of old growth forests at Itasca Park than it was in undisturbed old growth or near windthrow areas (Fig. 3.2). However, *I. pini* abundance declined markedly in 1998 and there was no longer any effect of disturbance history on local abundance *I. pini*. *I. grandicolli*s also showed an increase in their abundance in response to windstorm disturbance, but in this case, abundance was elevated at sites both within and near the site of windstorm disturbance, and the effect persisted through at least 1998 (Fig. 3.2). (Note that the abundance of *I. grandicollis*, the predator, *Thanasimus dubius*, and to a lesser extent, *I. perroti*, was underestimated in 1997 because the sampling was not implemented until after the peak flights for these species; Fig. 3.3.) *I. perroti* did not show any obvious responses to previous windstorm disturbance in either 1997 or 1998 (Fig. 3.2).

From July - September 1997, the abundance of *Thanasimus dubius*, the most important specialist predator of Ips, was lower in sites near blowdowns than anywhere else, including sites within the blowdowns (Fig. 3.2). Thus, the cumulative effect of disturbance on *I. pini* and *T. dubius* was that the abundance of prey relative to predator was markedly increased within and near windthrow areas of old growth forest (Table 1.1). Consequently, the potential for predator regulation of *I. pini* was reduced both within the blowdowns (due to increases in *I. pini*) and near the blowdowns (due to decreases in *T. dubius*) (Table 1.1). Presumably, the abundance of predator was reduced in forests adjacent to blowdowns because they were drawn into the blowdown areas by strong pheromone plumes from logs being colonized by *Ips*. Thus, the indirect effect of windstorm disturbance on I. pini and their predators can extend >200 m into the adjacent undisturbed forest. *I. grandicollis* differed from *I. pini* in that their abundance was increased by blowdowns over a larger area and for a longer time. Presumably, the larger spatial effect is because *I. grandicollis* tends to disperse more widely than *I. pini* and the greater longevity of the effect is because most *I. grandicollis* have only a single generation per year at Itasca, compared to 2-3 generations per year for *I. pini*. These results indicate that healthy pine within at least 200-300 m of blowdowns may be at risk for at least two years as a result of local increases in the abundance of *I. pini* and *I. grandicollis*, and correlated decreases in the abundance of predators relative to prey

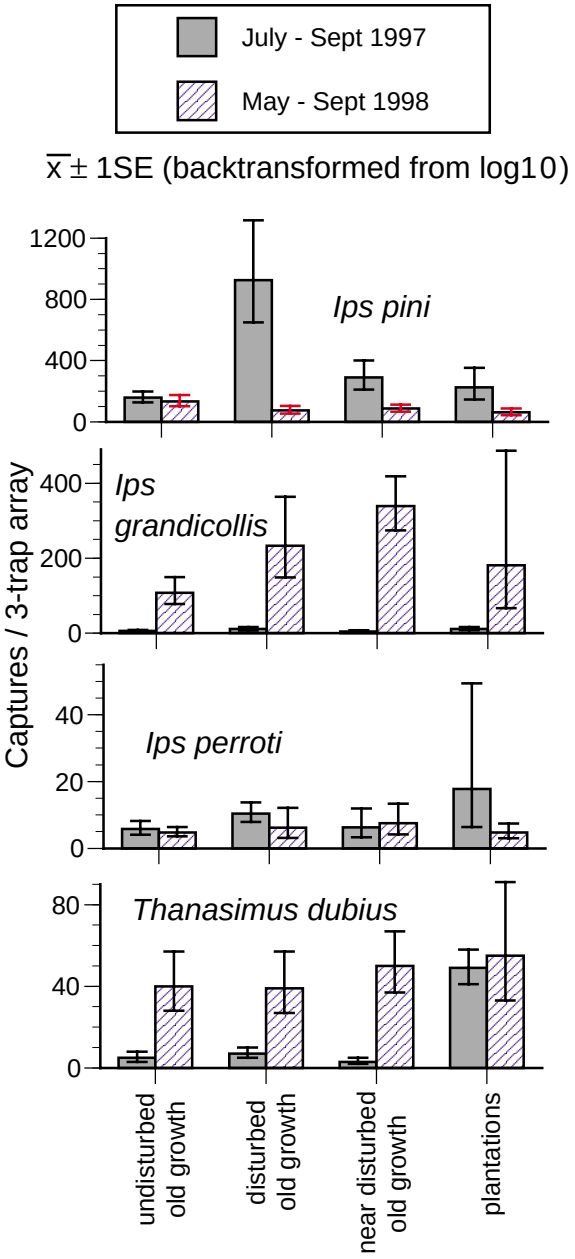

Fig 3.2. Abundance of *Ips* and their chief predator in old-growth pine stands at Itasca State Park with recent blowdowns (disturbed old growth), within 200-300 m of recent blowdowns (near disturbed old growth), and separated from the nearest blowdowns by > 500 m (undisturbed old growth). We also sampled in red pine plantations outside the park that contained younger trees (35 - 80 years old) and were 2 - 20 km from the nearest pine blowdowns.

Table 3.1: Relative abundance of predators (*T. dubius*) and prey (*Ips* spp.) in undisturbed old growth forest, old growth forest with windthrows in 1996-97, old growth forest near windthrows, and pine plantations near the park.

	Number of predators			
	Undisturbed	Disturbed	Near dist..	Plantation
Observed	163	46	18	212
Expected [a]	93	232	55	59
Prey / predator	15	129	78	7

[a] based on the null hypothesis of equal predator : prey ratios
Chi-square = 628.60, df = 3, P < 0.0001

The abundance of *I. pini* peaked during late summer, mid-September, while the abundance of *I. grandicollis* peaked in early May, and that of *I. perroti* peaked in August (Fig. 3.3). These patterns are similar to what we have typically observed during about ten years of similar sampling in west central Wisconsin, where we have additional information from direct observations of development in immature beetles and sampling throughout the year of adult colonizers in logs. Our interpretation of the data from Itasca is that most *I. grandicollis* have a single generation per year, but that some individuals of *I. grandicollis* go through a second generation (indicated by the small rise in trap captures during late 1998). In contrast, *I. pini* apparently complete two - three generations per summer: captures in May represent adults that successfully overwintered (parental generation); captures in late July represent their adult progeny (F_1 generation); captures in September represent their progeny (F_2 generation). *I. pini* captured the subsequent spring will be a mix of the F_2 generation that deferred reproduction and entered diapause directly plus progeny of the F_2 generation (F_3 generation) that completed development to adults during autumn of the Wisconsin. During 1998, maximum abundance of *I. pini* was about twice that of *I. grandicollis* and about 8 times that of *I. perroti* (Fig. 3.3). Captures of both of the most abundant specialist predators, *T. dubius* (Coleoptera: Cleridae) and *Platysoma cylindrica* (Coleoptera: Histeridae) were greatest in May and then remained at low levels throughout the rest of the summer. This temporal pattern matches our observations in west central Wisconsin and indicates these predators are much more likely to prey upon *I. grandicollis* than *I. pini*. Based on our studies in Wisconsin, we believe that *T. dubius* has but a single generation per year at Itasca, and that the captures of *T. dubius* adults in late summer represent a proportion of the population that completed development the previous year and remained in diapause as prepupae throughout the first part of the summer.

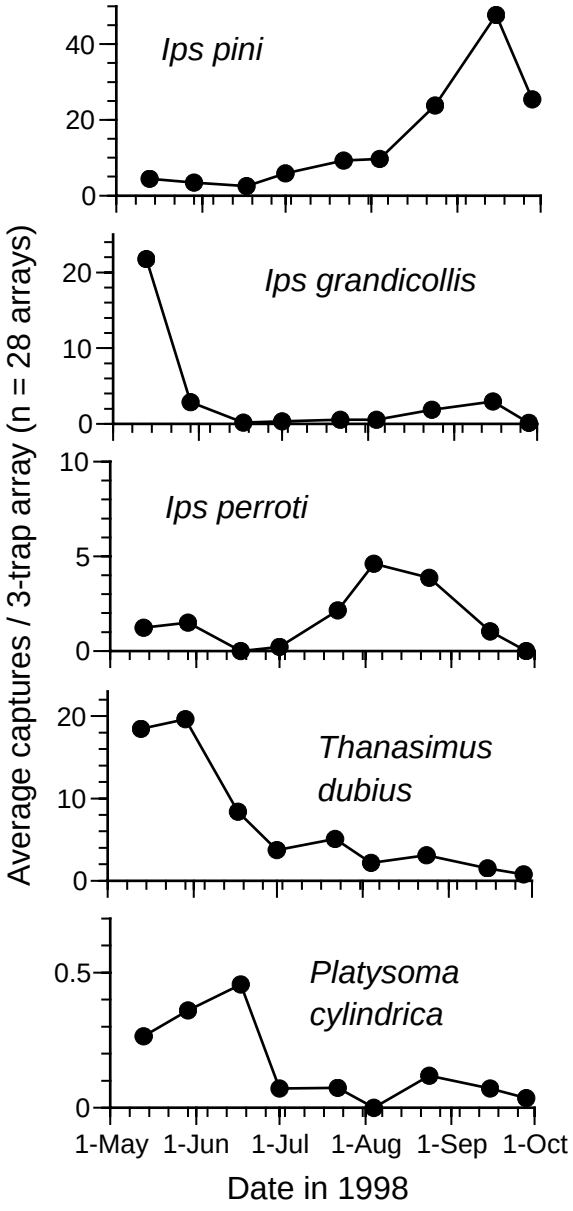

Fig. 3.3. Seasonal patterns in trap captures of *Ips* bark beetles and their chief predators at Itasca State Park

Across sites within the old growth forest, the abundance of *I. grandicollis* was positively correlated with that of *I. perroti*, but not with that of *I. pini* (Fig. 3.4), suggesting that the local abundance of the two most common bark beetles (*I. pini* and *I. grandicollis*) is determined by different factors. The local abundance of *T. dubius* was positively correlated with that of *I. grandicollis* but negatively correlated with that of *I. pini* (Fig. 3.5). Furthermore, the local abundance of both species of *Platysoma* predators were positively correlated with the abundance of *T. dubius* (Fig. 3.6) and *I. grandicollis* but not *I. pini*. It appears that the local abundance of specialist predators tends to be influenced by the abundance of *I. grandicollis*, presumably because *I. grandicollis* are the most abundant prey when *T. dubius* adults are feeding and reproducing in May. Conversely, the negative correlation between *I. pini* and *T. dubius* (Fig. 3.5 upper) suggests that *T. dubius* predation may sometimes limit the population size of *I. pini*. It is possible for *T. dubius* populations could simultaneously respond to the abundance of one prey species (*I. grandicollis*) and control the abundance of a second prey species (*I. pini*) if they prey upon both species but exert greater per capita impacts on the second species.

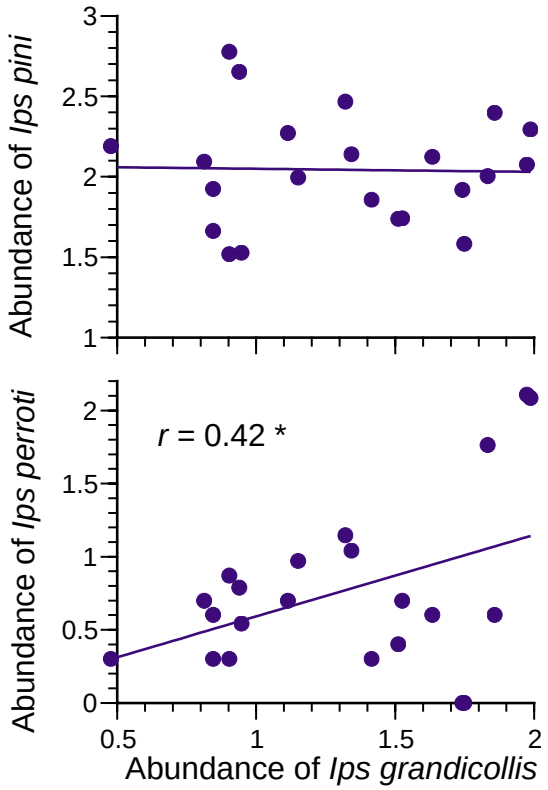

Fig 3.4. Correlation across stands of old growth forest between the abundance of different species of *Ips*

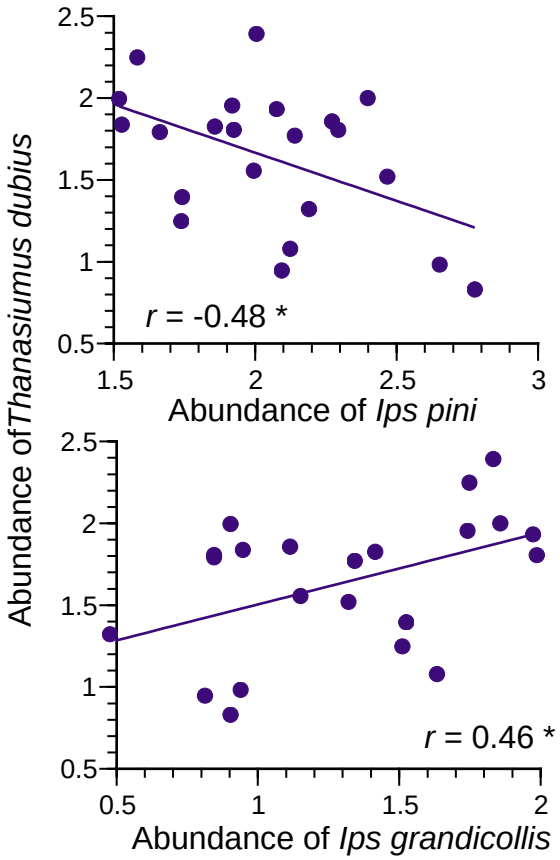

Fig 3.5. Correlation across stands of old growth forest between the abundance of *Ips* and their most common specialist predator, *Thanasimus dubius*

Competition among bark beetle species apparently tends to be reduced by the spatial and temporal separation of the three species, but they nonetheless overlap extensively in their resource use, and food resources are frequently limiting. So it seems probable that increased abundance of any one of the three species would tend to lower reproductive success of the other species. It is generally thought that of these species, *I. pini* is the most likely to kill trees. However, only limited evidence supports this belief and we observed all three species attacking live trees at Itasca. To the extent that *I. pini* is the most significant forest pest, *I. grandicollis* and *I. perroti* can be thought of as natural control agents of *I. pini*. Alternatively, if *I. grandicollis* is equally likely to attack live trees, then mass-trapping of *I. pini* may allow compensating increases in the abundance of *I. grandicollis* (because of relaxed competition from *I. pini*) and provide no net benefits in reducing tree mortality.

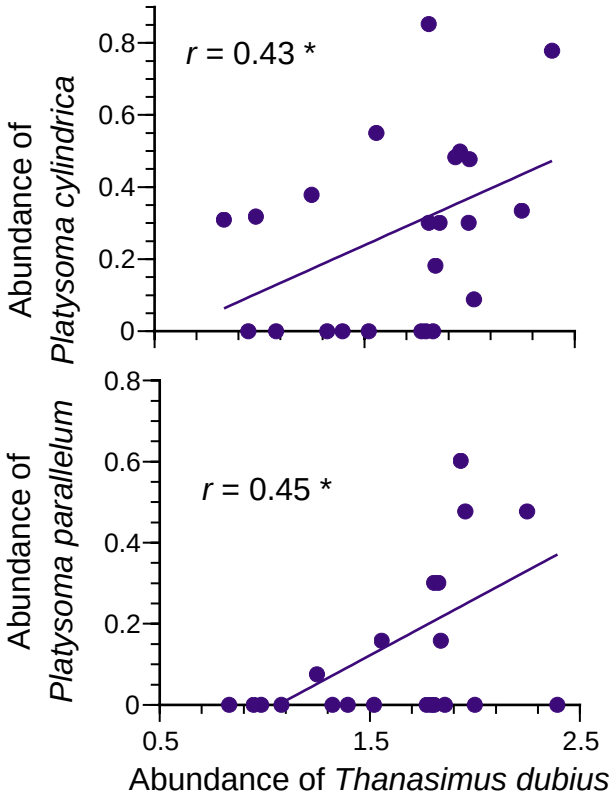

Fig 3.6. Correlation across stands of old growth forest between the abundance of the most common specialist predators of *Ips*, *Thanasimus dubius* (Cleridae) and two species of *Platysoma* (Histeridae).

These results allow some inference about the scale of beetle movements. Preliminary interpretations suggest that the effects of windthrows on *Ips* populations was restricted to within 200-300 m of the disturbance. This is also consistent with empirical studies of bark beetle movement indicating that within continuous forests, most beetles disperse less than 500 m (Turchin and Thoeny 1993). The implication is that beetle control programs or risk mitigation measures in response to blowdowns could be effective when conducted on a scale of hectares and need not be conducted across many square kilometers. One other practical implication is that forests outside the park suffer little risk of outbreaks due to beetle population fluctuations within the park.

Trapping results indicate that 3-trap arrays baited with 3 different combinations of commercially available pheromone blends provide an efficient protocol for quantifying the abundance of the most numerically important members of the bark beetle community at Itasca State Park (Fig. 3.7). A racemic blend of ipsdienol plus Lanierone captured primarily *I. pini*. Ipsenol by itself captured primarily *I. grandicollis* and ipsdienol + ipsenol captured primarily *I. perroti*. *Thanasimus dubius* and *Platysoma cylindrica* respond about equally to all three pheromone combinations, indicating that they are potential predators of all three species (although they overlap more in space and time with *I. grandicollis* than with *I. pini*). *P. parallelum* was least common of these predators, but displayed a strong preference for the combination of ipsdienol + ipsenol, suggesting that it is specialist predator of *I. perroti*.

Modest sampling with different enantiomeric blends of ipsdienol (one 3-trap array at each of 4 sites) indicated that a blend of 75%-(+): 25%-(-) was most attractive to *I. pini*, followed by a racemic blend of 50%-(+): 50%-(-), and a blend of 25%-(+): 75%-(-). The relative attractiveness of the racemic blend was sufficiently high (and its cost sufficiently low) that this makes a good cost-effective pheromone blend for trapping *I. pini* populations at Itasca. All of these patterns in pheromone preferences match our observations in Wisconsin, indicating that the broad patterns in pheromone preferences of these species are relatively constant across the western Great Lakes region.

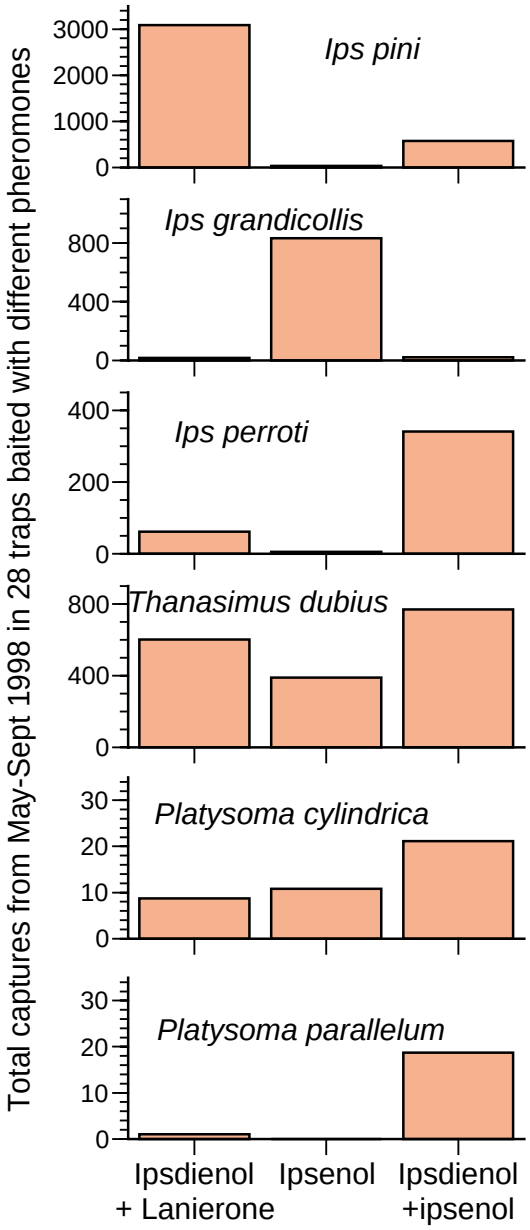

Fig 3.7. Captures of three species of *Ips* bark beetles and their most abundant specialist predators in funnel traps baited with different combinations of pheromones

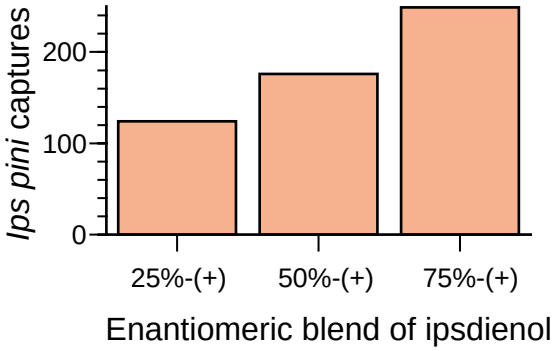

Fig 3.8. Captures of *Ips pini* in funnel traps baited with different enantiomeric blends of ipsdienol.

Conclusions. We recommend that low level sampling of bark beetle populations be continued each year at Itasca to monitor the relative regional abundance of bark beetle populations. Establishing 5-10 permanent trapping sites, with a 3-trap array at each site (each baited with either ipsdienol + lanierone, ipsenol, or ispdienol + ipsenol) would provide a valuable tool for assessing the risks from bark beetles that are associated with blowdowns or controlled burning. Controlled burning, which appears to temporarily exacerbate the risk to trees of bark beetle infestations could then be planned to follow summers in which the regional abundance of *Ips* is low, especially when low abundance during the summer is followed by winter conditions that will further lower the abundance of bark beetles (see Chapter 4). The logistics of establishing such a monitoring program would be quite easy now because of the availability of traps and trained personnel at Itasca.

Chapter 4
Cold tolerance and winter mortality of bark beetles at Itasca State Park

4.1 INTRODUCTION

Temperature has broad effects on the physiology and behavior of virtually all insects in all developmental stages. Temperature influences metabolic rate, flight activity, reproduction, nutrition, development, and survival. The ability to survive annual temperature minima can be a critical determinant of insect abundance. However, it is not known whether winter conditions exert significant mortality on populations of *Ips* bark beetles at Itasca State Park. In fact, surprisingly little is known about the overwintering biology of any *Ips* species. If winter conditions are a significant source of mortality for *Ips*, then it should be possible to reliably predict population abundance in the upcoming summer as a function of winter temperatures and snow cover. Such models could have high utility for management decisions. For example, controlled burning, which appears to increase the risk of bark beetle attacks (Chapter 6), could be planned to follow winters when beetle populations have been reduced by a particularly cold winter. Similarly, it might be desirable to place a priority on beetle control measures (e.g., mass-trapping or sanitation removal of winter blow downs) following mild winters when beetle populations are more likely to be high. This component of the research was designed to accomplish the following objectives: (1) measure the lower lethal temperature of the different species and life stages of *Ips*; (2) identify their overwintering sites; and (3) develop a model that incorporates knowledge of cold tolerance, overwintering sites, and microsite temperatures to predict winter mortality of *Ips* using easily measured climatic parameters (e.g., air temperature and snow depth). Appendix 6 is a related manuscript "Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America" which has been submitted to Environmental Entomology. Here we summarize the components that are salient to forest management at Itasca.

4.2 METHODS

Cold tolerance. We conducted field and laboratory studies to test the ability of beetles to survive at low temperatures. Supercooling points were measured by cooling individual insects at 0.20 °C / min and recording the temperature at which crystallization occurred (evident as an exotherm). Our studies included over 2500 measurements of supercooling points in *Ips pini*, *I. grandicollis*, and *I. perroti* of different life stages at different times during the winter and subjected to different acclimatization regimes. Because supercooling points are functionally synonymous with lower lethal temperatures for all of these species and life stages, the results provided a rather detailed characterization of cold tolerance in *Ips* spp. that inhabit Itasca State Park. These represent the first physiological measurements of cold tolerance that have been conducted for any of these species.

Logs infested by wild populations of *Ips* were collected in September 1997 and held in environmental chambers for one month at 10-15 °C under natural photoperiods. As adults emerged from logs they were introduced into screen boxes containing soil and litter and placed within the soil of a pine forest in Hanover, New Hampshire (43° 42' N, 72° 17' W). One box was removed from the soil each month for measurement of supercooling points in adults. One additional box containing 60 *I. pini* was placed in the forest at 1 m above ground where it was exposed to air temperatures without snow cover. Similar studies were conducted during the winter of 1998-99 and yielded similar results.

We tested for freeze-tolerance in association with the measurement of supercooling points. After we observed the exotherm associated with freezing, adults and immatures were warmed to ≈-22 °C and monitored for the ability to resume activity. Finally, we tested for the ability of immature *Ips* to resume activity and continue development after freezing. Logs with first instars and others with third instars and pupa were acclimated for one day at 15 °C, then one day at 8

°C, then one day at 0 °C before being exposed for seven days to -17 °C. After the -17 °C treatment, logs containing larvae were gradually warmed (1 day at 0 °C, then one day at 8 °C and one day at 15 °C before being moved to 22 °C) and placed into boxes containing a fresh log. Logs with first instars were dissected after 7 d at 22 °C to see whether early larvae had survived and resumed development. Remaining logs were examined after one month at 22 °C to see whether late larvae or pupae had completed development and begun to reproduce within the new log.

Overwintering habitats. In October 1998, 975 recently emerged *Ips grandicollis* and 284 *Ips pini* were introduced into litter of a 40-year-old *Pinus resinosa* forest at Colfax, Wisconsin and allowed to choose their overwintering microhabitat. To aid in locating the animals later, beetles were released within two 20-cm diameter PVC pipes that had previously being inserted into the soil with a minimum of disturbance to the soil and litter. In January and March 1999, pipes were removed with soil and litter intact and sliced into 2.5 cm and 1 cm sections respectively. Beetles within each of these depths were separated, identified, and scored as dead or alive.

Microclimate of overwintering habitats. In association with the studies of overwintering habitats, we collected detailed measurements of the microclimates experienced by overwintering beetles. From November 1998 through April 1999, air, litter, and soil temperatures were recorded every 30 minutes with an array of 28 thermisters spread among three 2 x 2 m sites with natural snow depth, no snow, or 2.5 cm of snow. The three climate study sites, and the studies of beetle overwintering habitat were all within 10 m of each other and within an area that was homogenous with respect to litter and soil characteristics. Snow was excluded from the no-snow site with an elevated lean-to. At the site targeted for 2.5 cm of snow, any snow in excess of 2.5 cm was carefully removed with a shovel within 24 h of deposition. Actual snow depth was recorded daily. Within each site, temperatures were recorded at the top of the litter, at the soil-litter interface (≈ 2 cm below the top of the litter), and at 1, 3, 5, and 8 cm below the soil-litter interface. Air temperature was recorded at 2 m. Some depths within some sites were measured with replicate probes. In all cases, the replicates provided very similar measurements (≈ 0.5 °C) and were subsequently averaged. Prior to analyses, raw data were processed further to yield daily minimum temperatures under each combination of soil depth and snow cover. After this data reduction, our climatic measurements yielded 1834 measurements of daily minimum temperatures across a range of snow depths and throughout the soil and litter profile that constitutes the overwintering habitat for adult bark beetles.

4.3 Results and Discussion

Cold tolerance. All three species of *Ips* that occur at Itasca were freeze-susceptible. No individuals of any species survived freezing. A few adults were able to move their antennae after freezing but otherwise never recovered normal movements. *I. pini* adults within a litter box exposed to New Hampshire air temperatures sustained complete mortality (100% of 60 individuals). Some immatures of *I. pini* and *I. grandicollis* survived temporarily following brief freezing but were apparently injured because they were unable to resume development. There was no survival of larvae or pupae in logs exposed to -17 °C for seven days; one month after treatment, logs contained a single fresh gallery that was excavated by one adult female and contained no eggs. In contrast, the control logs contained 13 new galleries with eggs and larvae. For all life stages of *Ips*, the supercooling point indicates the maximum cold tolerance. Under prolonged exposure to cold temperatures, some individuals die even though temperatures did not reach their supercooling point (Appendix 6), but no individuals ever survive temperatures below their supercooling point, and under most ecologically relevant climate scenarios, the supercooling point is functionally equivalent to the lower lethal temperature. Consequently, our measurements of supercooling temperatures in *Ips* provide a sound basis for evaluating the role of winter climate in the overwinter survival and population dynamics of *Ips* at Itasca State Park.

Ips adults were more cold tolerant than larvae or pupae (Tables 4.1-4.2). Eggs of *I. pini* had relatively high cold tolerance, with values similar to adults (mean ± SD = -15.6 ± 4.6 *n* = 7). Because immatures of *Ips* have less cold tolerance than adults, and because they are obliged to spend the winter within the phloem of their host trees, where they are poorly buffered from temperature extremes, we doubt that immatures of any species of *Ips* ever survive the winter at Itasca. In all likelihood, it is only the adults who have reached overwintering sites within the litter of the forest floor that survive to reproduce the following year. In many years, winter mortality of *I. pini* immatures may be significant at Itasca. *I. pini* reach their maximum abundance in late summer, and even in September, many adults are still laying eggs. Any progeny that do not complete development pupation before the the first day when air temperatures drop below about -15 ° C, will probably die. Consequently, the timing of the fall reproduction in *I. pini*, and the number of warm days that follow, probably has a strong impact on the abundance of *I. pini* the next year.

Table 4.1. Lower lethal temperatures (°C) of overwintering adults of three species of *Ips* that inhabit Itasca State Park. Values are mean supercooling point ± SD and sample size.

Species	Lower lethal temperature
I. pini	-12.6 ± 5.7 (496)
I. grandicollis	-15.2 ± 4.0 (195)
I. perroti	-14.4 ± 5.0 (32)

Table 4.2. Lower lethal temperatures (°C) during winter of immature life stages of *Ips* bark beetles that inhabit Itasca State Park. Values are mean supercooling point ± SD and sample size.

	Pupae	Larvae
I. pini and *I. grandicollis*	-8.3 ± 3.4 (176)	-9.6 ± 4.0 (66)

Across all our measurements of cold tolerance during the winter months, the supercooling point of *I. pini* adults, *I. grandicollis* adults, and *I. perroti* adults averaged -12.6, -15.2, and –14.4 °C (Table 4.1). There were some seasonal patterns in the supercooling point of *Ips* adults. For example, in 1997- 98, the average supercooling point of *I. pini* adults reached a minimum of about -16 ° C during autumn, and then increased by mid-winter to values of about -12 °C, and remained there throughout the spring and summer until the next autumn (Appendix 6). Adults of *I. grandicollis* and *I. perroti* also showed a tendency to have lower supercooling points in autumn than winter. Seasonal adjustments in the lower lethal temperature in *Ips* are probably an adaptive response to climatic patterns in the Great Lakes states. For insects that overwinter in the forest litter, snow cover provides a strong buffer against low temperatures. Consequently, the greatest risk of mortality from low temperatures comes from the combination of no snow and low temperatures. In Bemidji, there is a window of one month during the autumn when the probability of no snow is > 0.2 and air temperatures can drop below -20 °C (2 November to 2 December; see climatic analyses in Appendix 6). During most years, air temperatures drop below the lower lethal temperature for *Ips* adults sometime during November (mean ± SD of November minimum air temperature = -23.2 ± 6.0). Based on the same climatic criteria, there also appears to be a window of vulnerability to freezing during spring (25 March - 7 April in Bemidji), but we saw no evidence in either year of increased cold tolerance during spring. An assortment of experiments with different acclimatization regimes indicated that cold tolerance in *Ips* is unaffected by temperatures encountered during the previous hours, days, or weeks. Apparently, seasonal changes in cold tolerance are regulated by photoperiods or endogenous rhythms, and are not a direct response to changing temperatures.

Overwintering habitats. When allowed to choose their own overwintering microhabitats, most *I. pini* adults moved to within 1 cm of the bottom of the litter layer, which was ≈ 2 - 3 cm deep and comprised chiefly of pine needles (Table 4.3). In the January sample, 78% of 210 *I. pini* were beneath the litter layer, compared to only 19% of 573 *I. grandicollis*. The majority of *I. pini* had burrowed about one body length into the sandy soil below the litter layer while *I. grandicollis* almost never burrowed into the soil beneath the litter. *I. pini* were also in deeper microhabitats than *I. grandicollis* in the March samples (Table 4.3).

Table 4.3. Overwintering microhabitats of *I. pini* and *I. grandicollis* adults in January and March 1999.

	Ips pini			*Ips grandicollis*		
Depth below litter surface[a] (cm)	Number	% alive	% in stratum	Number	% alive	% in stratum
January 1999						
< 2 - 3 (litter)	47	55	22	465	85	81
2.5 - 5	163	82	77	108	88	19
5- 7.5	2	50	1	0	0	0
7.5 - 12	0	0	0	0	0	0
March 1999						
< 1	1	0	1	3	100	1
1 - 2	6	50	8	128	89	32
2 - 3	46	98	64	247	99	61
3 - 4	19	100	26	24	100	6
4 - 6	0	0	0	0	0	0

[a] Litter was ≈3 cm of pine needles

Microclimate of overwintering habitats

We used our microclimatic data to develop an empirical mathematical model that could estimate temperatures within the overwintering habitat of *Ips* adults. We evaluated an assortment of different statistical models, but found that one relatively simple model could accurately predict soil temperature profiles using only snow depth and minimum daily air temperature.

$$Y = B_0 + B_1 \cdot Air \cdot \left(\frac{-a \cdot snow}{1 + a \cdot snow} + 1 \right) \quad \textbf{Eq. 4.1}$$

where:

Y = minimum daily soil temperature,
B_0 = 0.60,
B_1 = $e^{-0.176} \cdot X^{-0.457}$,
a = $e^{-1.07} \cdot X^{-0.470}$,
X = soil depth (in cm) + 1,
Air = minimum daily air temperature (° C), and
$Snow$ = snow depth (in cm).

This model explained 74% of the variation in minimum daily soil temperatures. The statistical model was highly significant ($P < 0.001$ for each parameter and the model as a whole). Estimation errors from the model averaged < 0.7 °C, and seldom exceeded 2.0 °C. Models that also included minimum daily air temperatures on 1-2 d previous to the day of estimation provided only slightly better fit and were rejected in the interest of parsimony. Equation 4.1 produces estimates that are slightly biased with respect to day of the winter (estimates average ≈1 °C too cool in the early winter and ≈1 °C too warm in the late winter, presumably because the model does not account for the gradual loss of stored heat from the forest soil as winter progresses). This bias can be removed with models that incorporate day of the winter or cumulative cooling degree days, but the modest gain in precision did not warrant the additional complexity for our applications.

Fig. 4.1 uses equation 4.1 to depict soil temperature profiles as a function of air temperature under conditions of no snow, 5 cm of snow, and 10 cm of snow (upper panels of Fig. 4.1) and to predict soil temperature as a function of air temperature and snow depth at either 0 cm soil depth, 2.5 cm soil depth, or 5 cm soil depth (lower panels of Fig. 4.1). With no snow, minimum daily temperatures in the upper litter layer of the forest floor (0 cm soil depth) nearly match air temperatures. However, at soil depths greater than about 2 cm, microclimates are quite well buffered against the extremes of air temperature (e.g., at 2.5 cm soil depth, even with no snow, a minimum daily air temperature of -45 °C only corresponds to minimum soil temperature of -21 °C). In the upper soil, snow cover provides a strong buffer against extremes in soil temperature. With 5 cm of snow, a minimum daily air temperature of -45 ° corresponds to a minimum temperature at the top of the soil litter (0 cm soil depth) of only -13 °.

We combined our measurements of lower lethal temperatures in beetles (Table 4.1), beetle overwintering behavior (Table 4.3), and soil temperature profiles (Equation 4.1 and Fig. 4.1), to identify the conditions under which winter temperatures would exert significant mortality on bark beetle populations. A graphical analysis indicates that conditions of no snow, with minimum daily air temperatures of less than -25 °C would exert some mortality on *Ips* adults in the upper soil strata (Fig. 4.2). Air temperatures of -40 °C, with no snow cover, would produce significant mortality even among beetles as far as 3-4 cm into the forest floor.

By making a few simplifying assumptions, we are able to calculate the mortality of *I. pini* and *I. grandicollis* adults during any real or hypothetical cold weather (Fig. 4.3). For example, during a cold snap where minimum air temperatures reach -35 °C, with no snow cover, we would expect 64% mortality among *I. pini* adults that are overwintering in the soil and 69% mortality among *I. grandicollis* adults that are overwintering in the soil. The mortality functions for *I. pini* and *I. grandicollis* ended up being quite similar (Fig. 4.3), because although *I. grandicollis* tended to be more cold tolerant (Table 4.1), this was almost exactly compensated by their tendency to overwinter at slightly shallower depths in the soil (Table 4.3). Fig. 4.3 was constructed to allow easy estimates of the expected mortality for either species under any specified combination of snow cover and minimum daily air temperature. The model uses the mean and standard deviations of lower lethal temperatures for adults (Table 4.1), the distribution of beetle overwintering depths (Table 4.3, Fig. 4.2) and equation 4.1. The

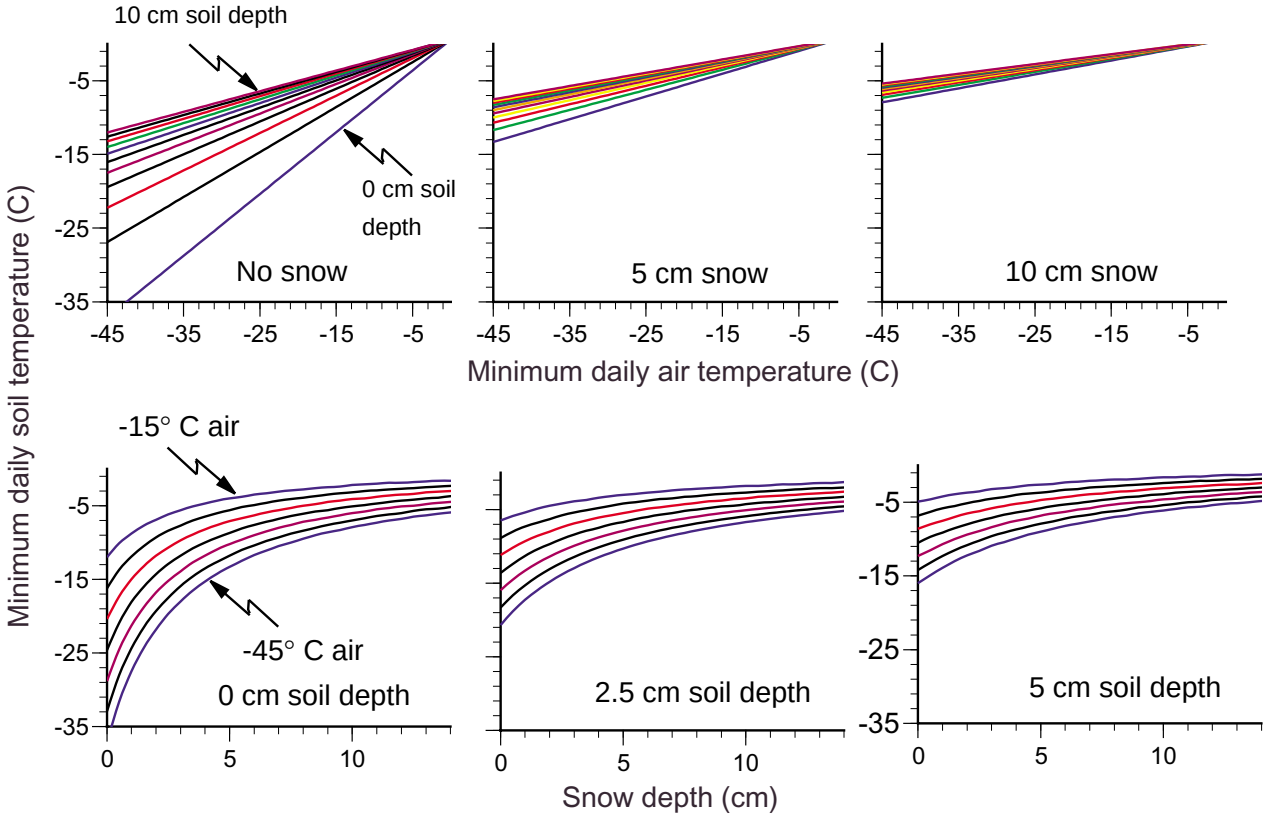

Fig. 4.1. Effects of air temperature and snow depth on soil temperature profiles in a red pine forest during winter. Response surfaces were calculated from Equation 4.1, which was estimated from empirical measurements of soil temperature profiles.

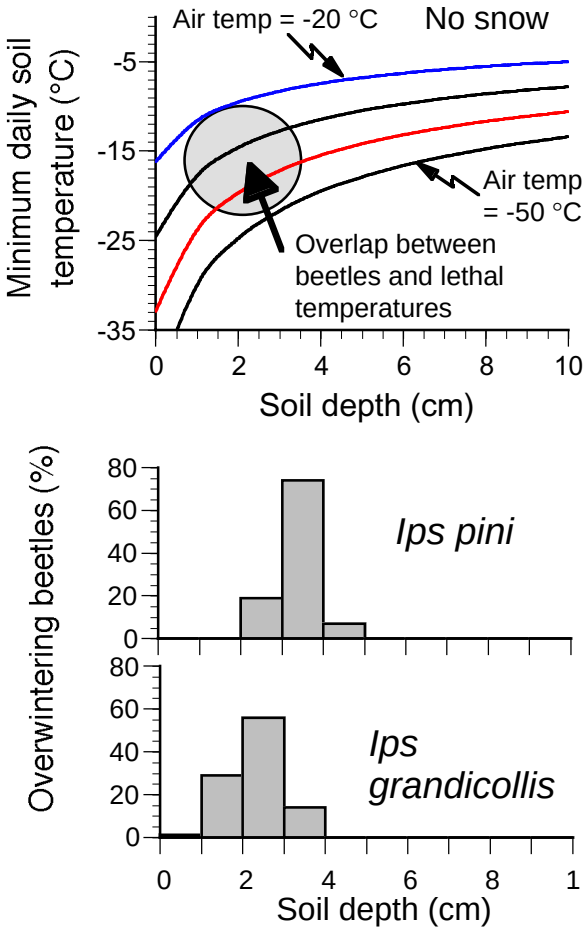

Fig. 4.2. Upper figure identifies the general combinations of soil depth and air temperature where winter soil temperatures can drop below the lower lethal temperatures for Ips adults (see also Figs. 4.1 and 4.3). Lower figure shows the depths at which I. pini and I. grandicollis adults overwinter (see also Table 4.3).

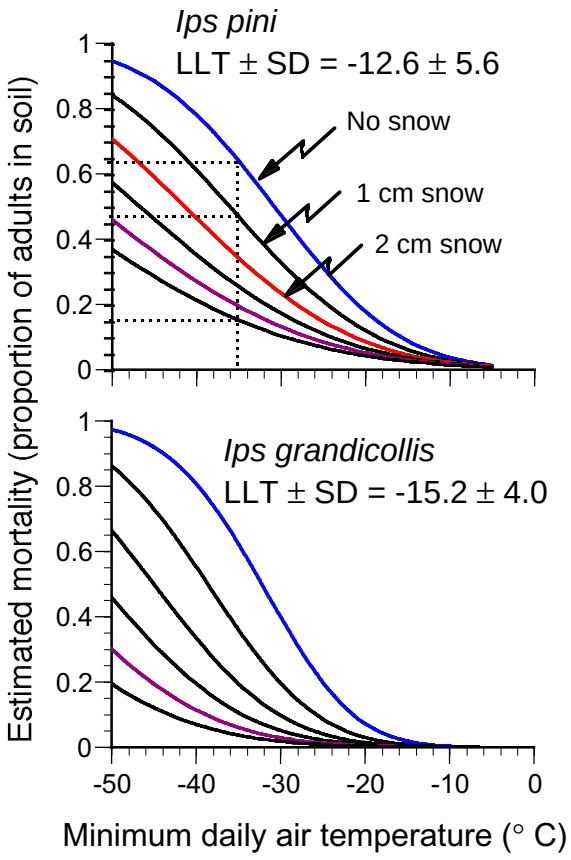

Fig. 4.3. Estimated mortality of overwintering *Ips* adults as a function of snow depth and minimum daily air temperature. Model incorporates physiological measurements of lower lethal temperatures, behavioral studies of microhabitat selection, and microclimatic measurements.

model assumes that lower lethal temperatures are normally distributed, that overwintering depth is independent of lower lethal temperature, and that lower lethal temperatures remain constant during the winter. We know that this last assumption is not strictly true (so the model tends to overestimate mortality somewhat in the autumn and underestimate mortality somewhat in mid-winter), but sensitivity analyses indicate that this bias is not very large. Other sensitivity analyses indicated that spatial variation in soil temperature profiles have negligible effects. The model implicitly ignores all life stages other than adults and any adults that have not gone into the forest soil; these assumptions are reasonable for the northern Great Lakes region, including Itasca State Park, because we are quite certain that the only *Ips* that can possibly overwinter successfully are those adults that leave their host trees and go into the forest soil before winter.

To assess the historical importance of winter temperatures for *Ips* populations at Itasca State Park, we used the model summarized in Fig. 4.3 to analyze climate records from 1948-1992 recorded at the the nearby weather station in Bemidji. For comparison, we performed comparable analyses for weather records from Eau Claire, Wisconsin, near our other bark beetle study site at Colfax, Wisconsin. During each year of the weather records, we used equation 4.1 to calculate the upper soil temperatures (0.5 cm depth) for each day of the winter, identified the

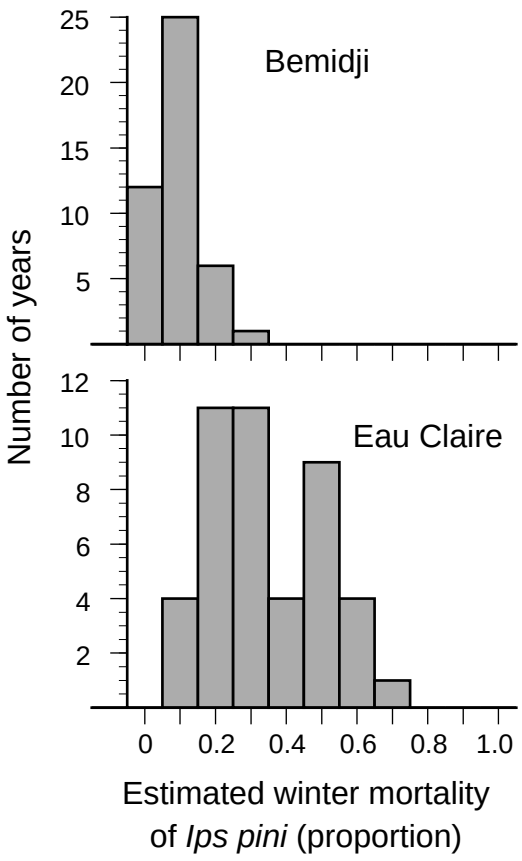

Fig. 4.4. Frequency distribution of estimated winter mortality of *I. pini* under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI.

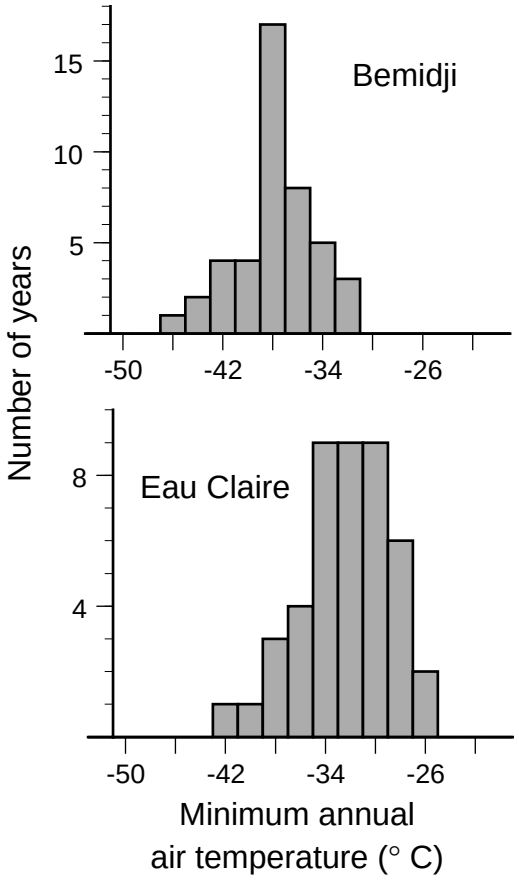

Fig. 4.5. Frequency distribution of minimum annual air temperatures under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI.

day when upper soil temperatures were minimized, and then calculated the percent mortality of *I. pini* for that day using the functions represented by Fig. 4.3. Surprisingly, these analyses indicated that winter mortality is more significant for *Ips* populations in west central Wisconsin than in Itasca State Park (Fig. 4.4). During a 45 year record, estimated winter mortality reached a maximum of only 33% under the Bemidji climate, compared to 71% under the Eau Claire climate (Fig. 4.4). This was in spite of the fact that minimum annual air temperatures were generally colder at Bemidji (Fig. 4.5).

However, snows tended to be earlier in Bemidji than Eau Claire, and the minimum soil temperatures are usually reached on the coldest day when there is no snow. In Eau Claire, it has been common to have snow-free days in December while this has been rare in Bemidji. The date of coldest upper soil temperatures in Bemidji has commonly been in November, while in Eau Claire, it tends to be in December (Fig. 4.6). As a result, minimum annual temperatures in the upper soil commonly drop below -20 °C in Eau Claire and seldom drop below -12 °C in Bemidji (Fig. 4.7).

Conclusions Because of the generally early snowfall at Itasca,winter mortality from cold temperatures is probably only important to resident *Ips* populations in some years. Fig. 4.3 provides an easy tool for identifying those winters. Probably no immature *Ips* ever survive the winter at Itasca, so the proportion of *Ips* populations that enter the winter as immatures in host material vs. as adults in the soil litter may exert considerable effects on population dynamics in most years. Management practices that influence the depth of the litter layer may influence overwinter mortality of *Ips* adults, because few overwintering adults burrow beyond the bottom of the litter, and the depth of the litter above them influences their microclimate. We hypothesize that prescribed burns will sometimes increase overwinter mortality of *Ips* adults because of the decreases in litter depth following fires. However, this suggestion should not be invoked as a rationale for prescribed burns without first conducting the appropriate experimental tests. We also point out that if reduced litter increases the mortality of *Ips*, it might also increase the mortality of beneficial insects such as *T. dubius* that also overwinter below the litter.

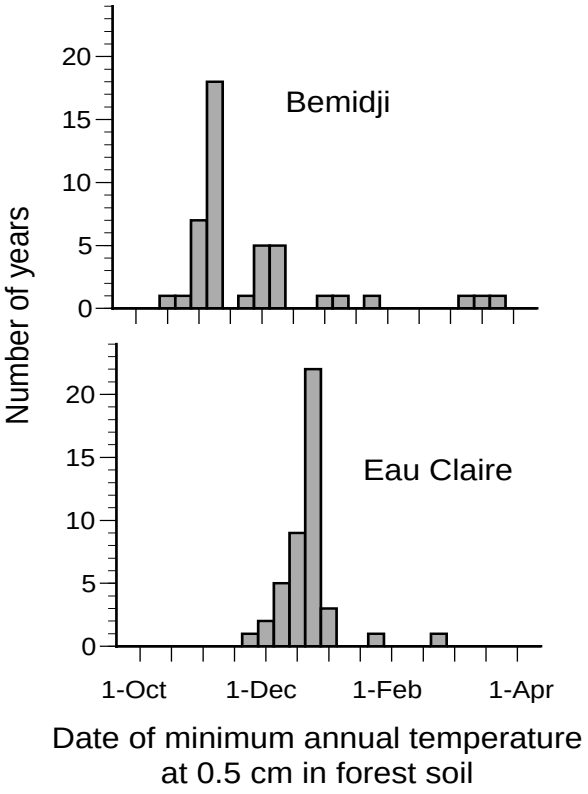

Fig. 4.6. Frequency distribution of the dates on which minimum annual temperatures were reached in the forest litter as calculated by Equation 4.2 under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI.

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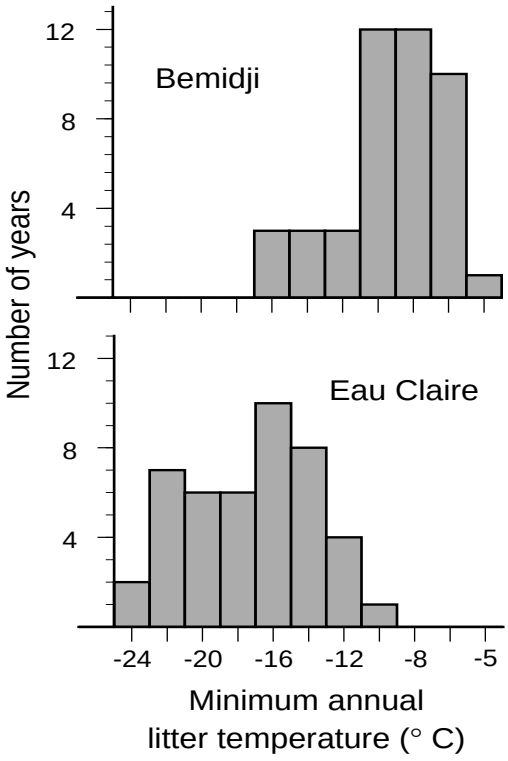


Fig. 4.7. Frequency distribution of minimum annual temperatures at 0.5 cm depth in the forest litter, as predicted using Equation 4.2 under historical climates (1948-1992) recorded at Bemidji, MN, near Itasca State Park, and Eau Claire, WI, in west central WI. Note that the date of minimum annual temperatures in the forest litter generally come earlier in the winter at Bemidji compared to Eau Claire (Fig. 4.6)

Chapter 5
Do bark beetles kill trees at Itasca State Park?

5.1 Introduction

Forest entomologists are mixed in their opinions of whether or not *Ips* bark beetles are a significant source of mortality for pine trees in the Great Lakes region. Most dying trees are infested by *Ips*, but this could be either because *Ips* cause the death of the tree or simply because *Ips* are efficient at locating and colonizing trees that are dying for other reasons. It has proven surprisingly difficult to distinguish between these two very different scenarios about the role of *Ips* in forest ecosystems. Which of these scenarios is true has important implications for forest management at Itasca State Park. If *Ips* infestations are restricted to trees that are destined to die with or without the presence of bark beetles, then the abundance of *Ips* has no consequences for the demography of pine forests at Itasca, and there is no compelling reason to monitor bark beetle populations, control them, or make any management decisions based upon the abundance of bark beetles. Alternatively, if *Ips* commonly attack and kill trees that are otherwise healthy, then bark beetles may deserve careful consideration in forest management decisions. This component of our research addressed the question of whether or not bark beetles kill trees at Itasca State Park. Our technical approach was to survey the population of red pines at Itasca for trees that were infested by bark beetles, monitor the fate of those trees, and evaluate whether the infested trees were in declining physiological condition prior to being infested by beetles. A variation on the central hypothesis was suggested by our observations in June of 1998 that many red pine trees exposed to the prescribed fires in April 1998 were under attack by bark beetles. This suggested the possibility that although *Ips* infestations may normally be restricted to trees that are otherwise dying, fire scorching may trigger beetle attacks in trees that are otherwise healthy. To test this possibility, we attempted to locate approximately equal numbers of infested trees for study that were and were not exposed to the prescribed fires of 1998.

5.2 Methods

In September 1998, we spent three days searching for, and examining, live mature red pine trees that were presently under attack by bark beetles. Our search was conducted by slowly driving all of the roads within Itasca State Park, and examining the crowns of red pines that were visible from the road, and well lit by the sun so that we could discern color patterns within the crown. Thus our surveys only included a small fraction of the old growth red pine stands within the park (probably less than 5%). Trees with crowns exhibiting symptoms of beetle attack (branches with red, dying needles, intermixed with healthy branches) were examined visually at ground level and with binoculars to the crown for the presence of bark beetles. Infested trees contained bark beetles within the inner bark or had bark beetle galleries and exit holes; most also had extensive recent bark punctures from woodpecker foraging, and often had fungal fruiting bodies growing out of the infested regions of the bark. Infested trees were marked, mapped, and photographed. To evaluate the growth history of infested trees, we extracted tree cores from each infested tree and from the nearest similarly sized red pine. Char heights were recorded for any infested trees that were exposed to the prescribed burn in spring 1998. Cores were also taken from 120 other old growth red pine trees (10 codominant trees from each of 12 sites; see Chapter 2) to allow comparisons of growth in infested trees with growth patterns of trees in the park at large. Analyses of mounted and sanded cores were done using WinDENDRO software (Regent, V 6.0.4) to determine yearly growth.

Annual radial growth years of each infested tree was graphically compared to its nearby uninfested control tree for the 60 years of growth ending immediately prior to the beetle infestation. We tested the statistical hypotheses that infested trees were experiencing declining growth during the last 5 - 10 years relative to their uninfested controls, and that this decline was less evident among infested trees exposed to fire, by first calculating a difference between each pair of trees for each year of the

growth record, which was standardized for historical differences in growth rates between tree pairs.

$$GD_{TY} = (GI_{TY}\text{-}GC_{TY}) - (GI_{35\text{-}84}\text{-}GC_{35\text{-}84}) \quad \textbf{Eq. 5.1}$$

where GD_{TY} equals the standardized growth for infested tree *T* in year *Y*, GI_{TY} is the radial growth for infested tree *T* in year *Y*, GC_{TY} is the radial growth for control tree *T* in year *Y*, $GI_{35\text{-}84}$ is the average radial growth of all infested trees from 1935-1984 and $GC_{35\text{-}83}$ is the average radial growth of all control trees from 1935-1984. Equation 5.1 has the property that the average GD_{TY} across all trees equals 0 for the period from 1935 to 1984. 1935 to 1984 was chosen somewhat arbitrarily because it provided a 50 year estimate of tree growth that was likely to pre-date the start of physiological deterioration under most scenarios of growth decline that could predispose a tree to beetle infestations in 1998. Thus, under the hypothesis that beetles are preying on declining trees that are destined to die soon anyway, we would expect that GD_{TY} would tend to become increasingly negative during the 5-10 years prior to beetle infestation (as infested trees declined in their growth relative to the uninfested control trees). Pathogens, root dieback, senescence, and shifts in the water table are mechanisms that could produce a pattern of physiological decline over this time scale that lead to imminent tree death with or without the involvement of bark beetles. All of these mechanisms, and most others that we can imagine, would usually be evident as marked decreases in tree growth during the years prior to death.

A related hypothesis, although the implications are different for forest demography, is that bark beetles preferentially attack trees that are chronically slow growing. We tested this hypothesis by comparing the average growth rate of infested and uninfested trees during the pre-infestion time period from 1935-1984.

In September 1999, we revisited the infested trees that were marked in 1998, evaluated their condition, and photographed them. At this time, we also recorded the number of newly infested trees that we observed while searching approximately the same area as in 1998.

5.3 Results and Discussion

Symptoms of infested trees. In 1998, we located 41 trees that were either currently infested by bark beetles or had been infested during the previous months. Trees that were infested by bark beetles were often evident at a distance from examination of their crown. Infested trees were characterized by the presence of branches with red, dying needles, intermixed with healthy branches (Fig. 5.1, left and middle). The dying branches are those whose vascular connection has been interrupted by beetles girdling the inner bark of part of the trunk. Upon closer examination, infested trees contained bark beetles or bark beetle galleries within the inner bark of the lower bole, had beetle frass and sawdust sprinkled around the base of the tree, and/or had bark beetle exit holes farther up the bole of the tree that were evident with binoculars; most infested trees also had extensive recent bark punctures from woodpecker foraging (usually Black-backed Three-toed Woodpeckers, *Picoides arcticus*, which appears to specialize in foraging on trees recently infested with bark beetles) and often had fungal fruiting bodies growing out of the infested regions of the bark. Fig. 5.1, right, shows a tree with a fading crown that was not infested by beetles. In this case, the crown deterioration was quite uniform, without the mosaic appearance of dying and healthy branches that is often produced by beetle infestations; this tree was probably afflicted with Diplodia blight (*Sphaeropsis sapinea, = S. ellisii = Diplodia pinea*.). Our surveys revealed only one or two mature red pine that appeared likely to die as result of Diplodia blight or any other pathogen. Our impression was that pathogens are a minor cause of mortality in mature trees compared to bark beetles.

All of the infested trees were of codominant crown size class (none were intermediate or suppressed). Infested trees were scattered throughout the areas of pine forest that we searched, although there were some areas where infestations were concentrated (Fig. 5.2). Thirteen of the infested trees were within the area burned in April 1998; char heights on these trees ranged from 0.2 to 5 m (mean ± SE = 1.83 ± 0.10 m). With more time, we could have certainly found many more infested trees, especially within the burned area, where many

For images see
http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm

Fig. 5.1. Mature red pines at Itasca State Park that were under attack by *Ips* bark beetles during 1998 (left and middle). Note the presence of branches with red, dying needles intermixed with healthy branches. Contrast with the uniformly thinning crown of the tree on the right, which was not infested with bark beetles (possibly infested with Diplodia blight). The tree on the left, 704 in Table 5.1, was dead in 1999. The middle tree, 720 in Table 5.1, was sustaining continued attacks in 1999.

trees were attacked by bark beetles within the scorched area of the lower bole (see Chapter 6).

It was not always possible to identify the beetle species with certainty because often the infested areas of the bole were out of reach many meters above ground. However, it appeared that *Ips* spp. were the dominant bark beetles in the majority of infested trees. We found *Ips pini*, *I. grandicollis*, and *I. perroti* infesting live trees, suggesting that all three *Ips* species are sufficiently aggressive to impact tree survival (although the only *I. perroti* specimens were from fire-damaged trees). In many cases, we found two or more species of *Ips* intermingled within the same tree, suggesting that they may cooperate in mass attacks (and implying that increases in the abundance of one *Ips* species may sometimes benefit the reproductive success of other *Ips* species). The other bark beetles that we found infesting live red pines at Itasca were: *Dendroctonus valens* (common), and *Polygraphus rufipennis*, *Trypodendron lineatum*, and *Xyleborus dispar* (occasional). *D. valens* probably contributes to early attacks on many trees. The latter three species appeared to be secondary colonizers that generally depend upon the more aggressive species to first kill the host tree.

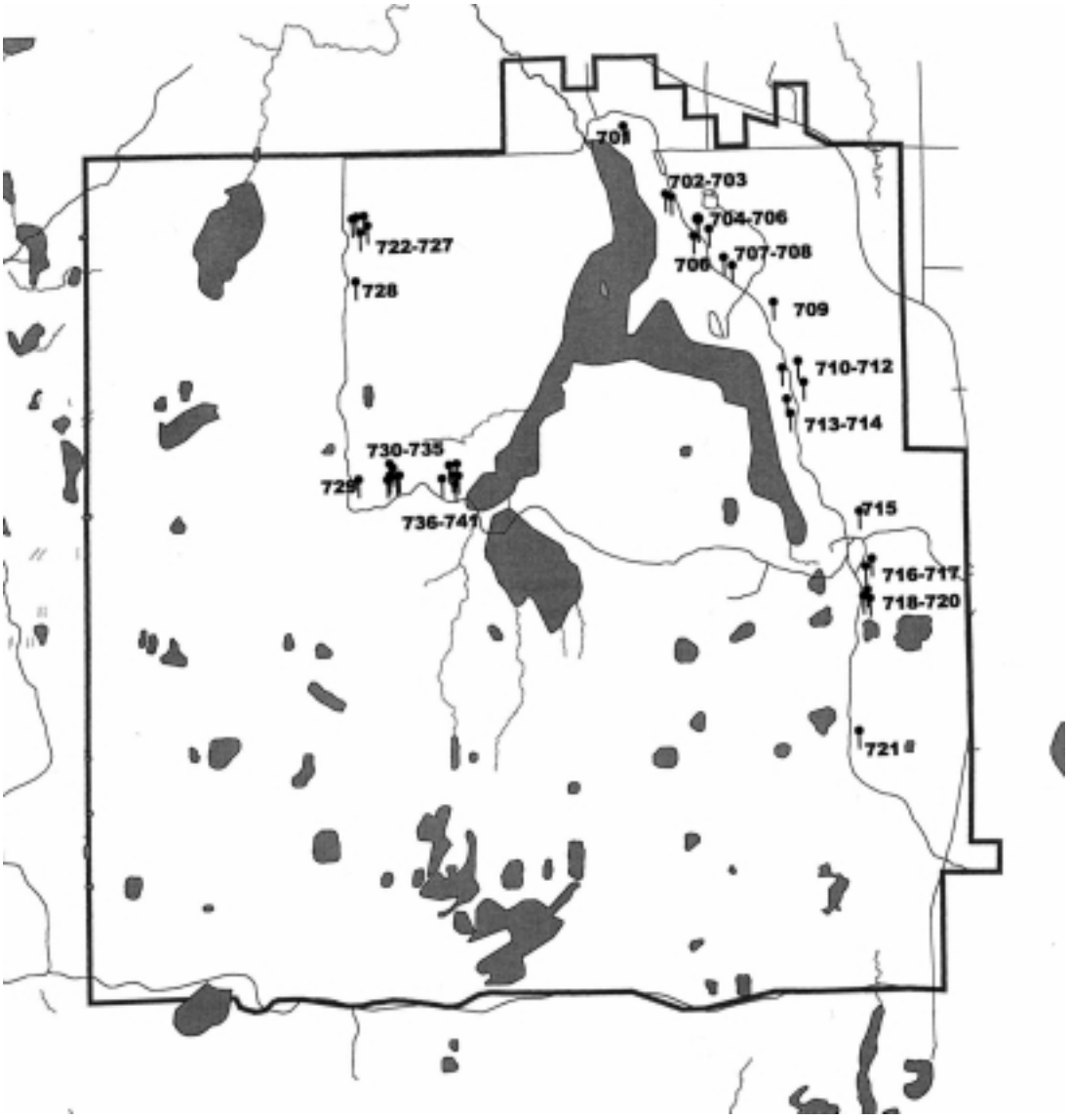


Fig. 5.2. Location of beetle-infested red pines that were marked and measured in 1998.

For images see
http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm

Fig. 5.3. Red pines attacked by bark beetles at Itasca State Park. Photos are of the same trees taken in Setember 1998 (left) and September 1999 (right). Upper tree (713 in Table 5.1) was reduced to about 10% of its live crown by 1999, and will probably be dead by September 2000. Lower tree (724 in Table 5.1) sustained charring to 8 m on the trunk and was colonized within the scorched area by *Ips pini* during 1998. Copious resin flow restricted damage (see Chapter 6), but the tree was sustaining additional attacks in 1999. This tree may survive the attacks, but has been permanently girdled on a portion of the lower trunk, will develop a cat-faced scar if it survives long enough, and will more be susceptible to future fires (because of the loss of insulating bark and because the white pine next to it, which succumbed to the fire and subsequent attacks by bark beetles, will increase fuel loads during the next fire (Figs. 6.6 - 6.8).

Fate of infested trees. Of 41 mature red pines that were infested with beetles during 1998, 21 were dead by the end of the next growing season or were clearly going to be dead by the next year (Table 5.1). Of these, 18 appeared to have been killed by the beetles (Fig. 5.1) and three probably would have died from the fire damage alone. Of the 17 trees that were still alive, 6 of them were sustaining continuing beetle attacks in 1999, and 11 were apparently free of additional beetle attacks. In our judgment, some of the trees that were alive and no longer sustaining beetle attacks could survive for decades longer. However, all attacked trees sustained irrepairable damage to their vascular system, lost significant portions of their crown that had been supported by the damaged vascular tissue, and were in the process of losing portions of their bark, making them more vulnerable to pathogens, fire, windstorms, and future insect attacks (Fig. 5.3). Thus, beetle infestations led to rapid tree mortality in about 50% of the trees and increased the annual probability of mortality for the remainder.

In the process of revisiting infested trees that were marked in 1998, we identified 39 trees that became infested during 1999 - comparable to the 41 trees that we found in 1998. As in 1998, the newly infested trees were scattered throughout the park, but there were two notable concentrations of growing damage. In the vicinity of infested trees #707 and 708 (see Fig. 5.2), there were 11 mature red pines (out of a total of 15 in the immediate area) that were either recently dead or currently under insect attack. Examination of the main roots and lower boles of several of these currently infested trees showed no evidence of root pathogens or any problems with the root system. Bark beetles were the only apparent cause for tree mortality in this stand. (This site is immediately east of the park road at the sign "Douglas Lake Lodge, 3 miles"). The other obvious hot spot for beetle infestations was in the vicinity of infested trees #730-735 (see Fig. 5.2), which coincides with the red pine phytochemistry site #2, and is located just north of the park road, just beyond the advance sign for the largest white pine. Of approximately 200 trees at this site, there were 6 infested trees in 1998, seven more that became infested during 1999, and three more that were recently dead. There was no obvious cause for tree mortality at this site other than bark beetle infestations.

Previous growth vigor of infested trees. Of the 35 trees that were infested by bark beetles in 1998, none showed a pattern of declining growth in the years previous to the infestation (Fig. 5.4, Appendix 5). Overall, there were no systematic differences between infested trees and their paired control trees at any time during the 63 year growth record that was analyzed (Fig. 5.5). The average difference between the growth of infested and control trees was not significantly different from zero during any year from 1935 to 1997 (Fig. 5.5, upper). Neither was there any suggestion of a growth decline during the years immediately preceding beetle infestations in

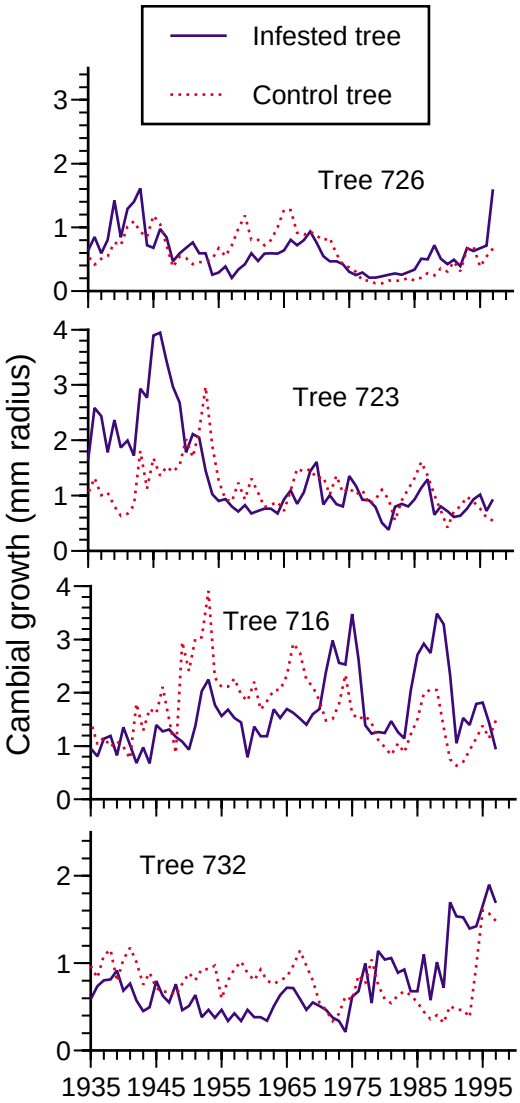


Fig. 5.4. Examples of growth rate comparisons between *Pinus resinosa* infested with *Ips* bark beetles in 1998 and paired non-infested control trees. None of 35 infested trees showed evidence of declining growth relative to the control tree in years prior to being infested by beetles. (See Appendix 4 for other trees)

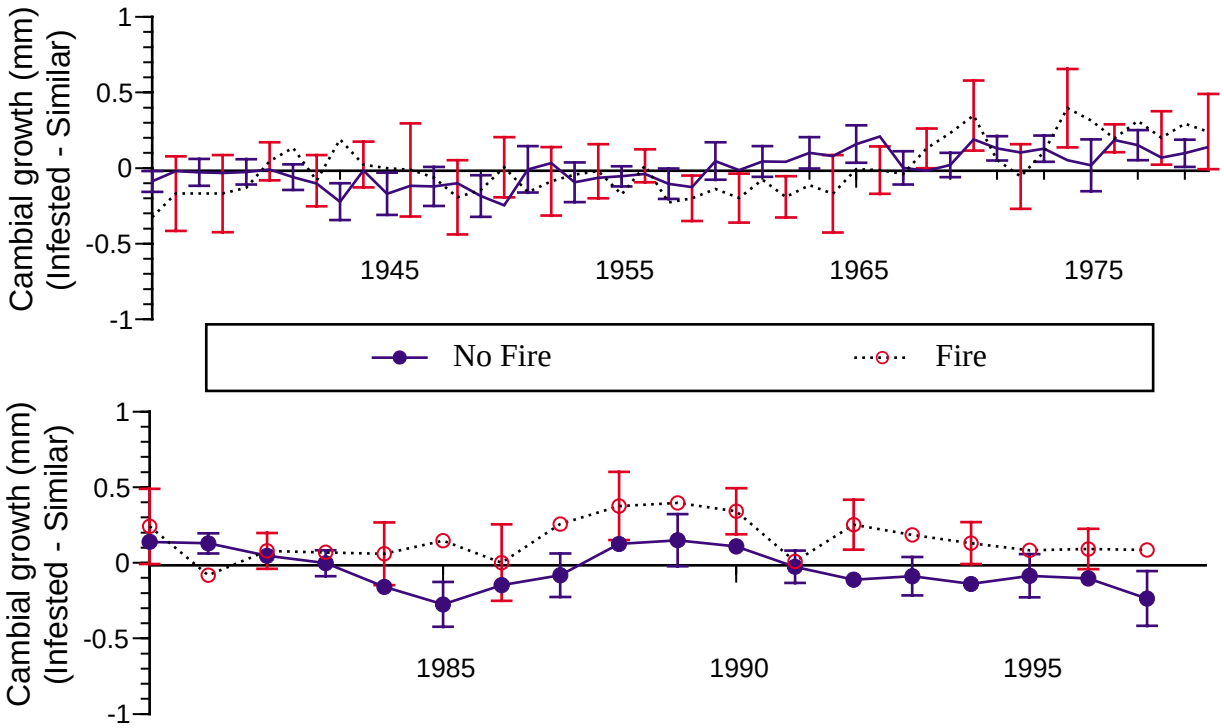


Figure 5.5. Mean growth differences between *Pinus resinosa* infested with *Ips* spp. bark beetles in 1998 and their paired uninfested control trees from 1935-1980 (upper) and from 1980-1995 (lower)

1998 (Fig. 5.5, lower; mean difference ± SE = 0.029 ± 0.026 mm / year; $T = 1.12$, $P = 0.26$). These patterns were the same for trees that were infested following fire scorching as for trees that were infested in the absence of fire.

Similarly, there was no evidence that bark beetles were tending to infest trees with chronically low growth rates. In fact, a comparison of the frequency distribution of growth rates for infested and uninfested trees showed that bark beetle infestations included some of the fastest growing trees in the park (Fig. 5.6; mean ± SE for infested vs uninfested trees from 1935 to 1984 = 1.09 ± 0.084 vs. 1.06 ± 0.041 mm / year, n = 35 and 121).

Conclusions. These data provide compelling evidence that *Ips* bark beetles commonly kill trees at Itasca. There was no suggestion of growth declines prior to beetle infestation in even one of the 35 infested trees for which we were able to reconstruct their growth history. Results also falsify the hypothesis that beetle infestations at Itasca are restricted to chronically slow-growing trees. Instead results indicate that *Ips* attacks are random with respect to tree growth. Even the most vigorously growing trees were subject to attack by bark beetles.

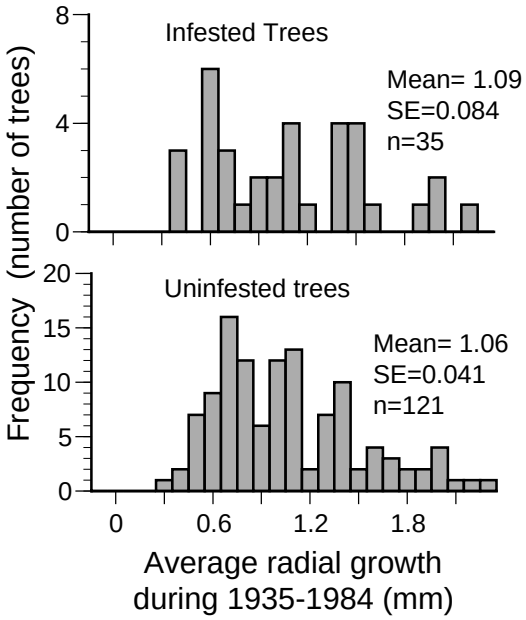


Fig. 5.6. Average growth rates during 50 years of trees subsequently infested by *Ips* in 1998 compared to those of uninfested trees.

Stalwart advocates of the hypothesis that *Ips* do not kill trees could still argue that there was some serious undiagnosed malady afflicting all of the infested trees in this study, which predisposed them to attack by beetles, and would have ensured that the trees would be dead within a few years anyway. However, virtually all of such potential maladies would be expected to produce a signal of reduced growth for at least a few years prior to infestation in at least a few trees out of 35. It seems most parsimonious to assume that many of the red pines infested by bark beetles at Itasca would otherwise live for decades longer.

We believe that we would find bark beetle infestations of living trees in almost any year at Itasca . The forests contain many standing dead trees at various stages of decay, indicating that tree mortality consistent with *Ips* infestations is common. We do not believe that the number of infested trees that we found were substantially elevated by the blowdowns during 1995-96. Our surveys were not specifically concentrated in stands that experienced blowdowns and many of the infested trees that we mapped were outside the immediate vicinity of any recent blowdowns. One notable exception was the cluster of infested trees mapped as 730-735 (Fig. 5.2), which were within 50 m of a substantial blowdown that probably produced tens of thousands of beetles during 1996-97. We guess that we would have found many more recently infested trees if we had specifically searched in the vicinity of similar blowdowns. It is noteworthy that *Ips* abundances were not at epidemic levels in 1998 or 1999, when most of our study trees became infested. In 25 3-trap arrays, mean captures of *Ips* did not exceed 145 beetles / site during any trapping period in 1997 or 47 beetles / site during 1998 (Chapter 3). Comparable sampling at our study sites in Wisconsin regularly capture a maximum of 50-100 beetles / site under apparently endemic conditions.

We estimate that our survey for beetle infestations included about 4000 trees. In both years, we found about 40 newly infested trees, suggesting that the annual probability of an individual tree becoming infested is about 1%. About half of the trees infested by beetles died in the short term, suggesting that the annual probability of a mature red pine dying from beetle infestations is about 0.5%. With an annual mortality rate of 0.5%, and no recruitment of trees, the Itasca population of red pines would be halved by beetle attacks in 139 years (Fig. 5.7). Of course, red pines also die from other causes such as windstorms, fires, pathogens, and lightning. If we guess that the background mortality rate from these other causes is 0.25% / year, and combine it with mortality from bark beetles, then it would require 93 years for the red pine population to be halved. This model still fails to account for the increased probability of future mortality that is a legacy of surviving past beetle infestations. Our data suggest that this increased risk is assumed by about 0.5% of the tree population per year. If we guess that the mortality rate of previously attacked trees increases to 5% per year, and hold the other estimates constant, then the tree population would be halved in 65 years. This halving time of 65 years can be contrasted to a hypothetical forest that lacks beetles (background mortality of 0.25% / year only), which would have a half life of 277 years. These calculations are simplistic in many respects, but they illustrate that the bark beetle attack rates we observed at Itasca during 1997-98 translate into important effects on the expected longevity of old growth red pine forests.

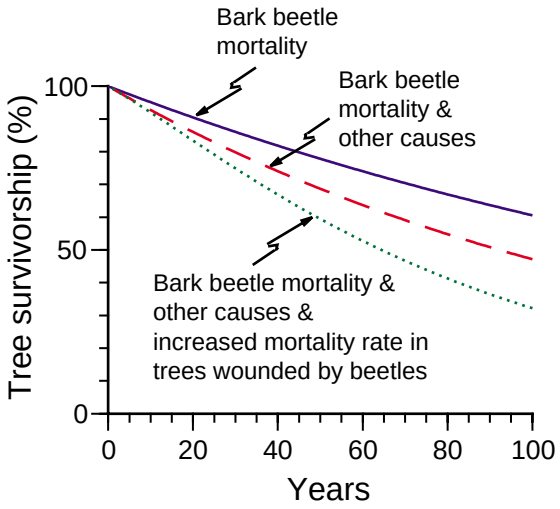


Fig. 5.7. Survivorship curves for a hypothetical population of red pines with a constant annual mortality rate of 5 trees / 1000 from bark beetles (estimated from our surveys at Itasca), or the same mortality rate from bark beetles plus a mortality rate of 2.5 trees / 1000 from other causes, or these same mortality rates plus an increase in mortality rates of trees previously wounded by bark beetles (to 50 trees / 1000). Under the latter scenario, which seems most realistic, the tree population would be reduced to half of its present size in 65 years.

Table 5.1. Summary of study trees infested by bark beetles that were marked and mapped in 1998.

Tree	DBH (cm)	Fire	Fate in 1999	Notes
701	49	no	Dead.	
702	68	no	Dead.	
703	56	no	Dead.	
704	71	no	Dead.	
705	75	no	Fully red crown. Dead by 2000.	
706	86	no	Attacks continue. 70% needle loss. Dead by 2000.	
707	85	no	No new attacks. 30% of crown lost.	
708	91	no	Attacks continue. Lower branches dead. Upper 30% of crown alive.	
709	95	no	No new attacks. Partly girdled.	
710	102	no	No new attacks. Girdled >50%.	
711	99	no	Dead.	
712	87	no	No new attacks. 70% needle loss. Death imminent.	
713	82	no	<10% green needles. Death imminent.	
714	87	no	No new attacks. Partly girdled	
715	62	no	Lower branches dead. Needles yellowing. Death imminent.	
716	81	no	Dead.	
717	47	no	No new attacks. Lower branches killed. Remaining crown OK.	
718	69	no	No new attacks. Half of crown dead. Girdled >50%.	
719	54	no	Dead except one branch at 10 m.	
720	76	no	New red branches. Continued attack.	
721	92	no	Dead.	
722	63	yes	No new attacks. Partly girdled. Thinning branches.	
723	86	yes	Dead.	Center burned out to > 4 m around; killed by fire, colonized by beetles
724	81	yes	New attacks. Incipient CFS*.	Scorched to 8 m
725	62	yes	New attacks. >70% girdled. 1 existing CFS*. Incipient CFS* on other side.	Scorched to 6 m; Old CFS* to 2 m
726	39	yes	New attacks. CFS* enlarging from 2 m, 25% circumference to 5 m, 50%.	Scorched to 3 m; beetle attacks expanding old CFS
727	74	yes	Lower crown dead.	Scorched to 4 m; beetle attacks expanding old CFS
728	78	yes	Dead.	Old CFS to 1.2 m; burned out trunk; killed by fire, colonized by beetles
729	?	no	Dead.	
730	72	no	New attacks. >50% girdled.	
731	65	no	<10% green. Functionally dead.	
732	99	yes	<10% green. Functionally dead.	Scorched to 3 m;
733	90	yes	No new attacks. 60% girdled.	Scorched to 70 cm
734	55	yes	Dead.	Scorched to 30 cm; old CFS* to 25 cm
735	52	yes	Dead. All needles red.	Scorched to 20 cm
736	64	yes	Dead.	

737	21	yes	No new attacks. >50% girdled.	
738	47	yes	No new attacks. >50% girdled.	Old CFS* to 2.5 m
739	61	yes	Dead.	
740	24	yes	Dead.	
741	23	yes	Dead.	Scorched to 5 m; old CFS* to 2 m

* CFS = cat-faced scar; see Chapter 6.

Chapter 6
Interactions between fire, bark beetles, and tree mortality

6.1 INTRODUCTION

Coincident with our bark beetle research program, prescribed fires began to be implemented at Itasca as a management tool to promote regeneration of red pine. Within six weeks following controlled burns in April 1998, we observed that numerous red pines within the burned area were being attacked by *Ips* bark beetles. Some of the attacked trees had sustained significant crown damage from the fire and were probably destined to die in 1998 with or without bark beetles. However, other infested trees were merely scorched on the outer bark of the lower bole, and had not sustained any crown damage from the fire, yet appeared to be endangered by the subsequent beetle attacks. Some of these trees died as an apparent result of the beetle attacks (Chapter 5). Many of the scorched red pines that were under attack exhibited copious resin flow around the sites of beetle attack. This was unusual because *Ips* bark beetles have low tolerance for pine resin and do not normally infest trees that are exuding resin. Evaluating the consequences of fire for bark beetle infestations was not part of our original research objectives. However, these observations, and a preliminary review of the literature, suggested the possibility for complex interactions between fire and bark beetles at Itasca that may be at least as important to forest management decisions as interactions between windstorm and bark beetles. Therefore, we include this chapter describing what we have been able to infer about interactions between fire, bark beetles, and tree mortality.

Fire management practices are changing in many forests throughout the world, partly in response to increased recognition of the undesirable effects that fire suppression can produce in some forests, such as loss of keystone tree species (Keane et al. 1990, Tomback et al. 1995, Williams 1998). In addition to its possible beneficial effects in promoting tree regeneration, prescribed fires may have some other benefits for forest ecosystems. In some cases, fires can reduce pest outbreaks (Hadley and Veblen 1993, Mutch et al. 1993, Herr et al., 1994, Jurgenson et al. 1997, Kipfmueller and Baker 1998). One mechanism by which fires can reduce pest outbreaks is by direct effects on insect populations (Sgardelis et al. 1995). For example, ground fires in mid-April in Itasca, might tend to kill bark beetles, which are in diapause within the forest litter at that time (Chapter 4). Indeed, fire has long been employed in agricultural and range systems to directly reduce populations of damaged insects (Miller 1978, Fellin 1980, Miller and Wagner 1984, Brennan and Harmann 1994). Fire can be an effective tool in controlling seed or cone-infesting insects (Miller 1978) and has sometimes been used as a strategy to reduce populations of bark beetles (Smith et al. 1983, Stock and Gorley 1989). However, some insect populations rebound rather quickly after fire (Collet 1998, Greenberg and MacGrane 1996) perhaps because fires also reduce populations of predators such as *Thanasimus dubius*, which also tend to overwinter in forest litter.

The net effect of fires on forest pests is difficult to predict because tree defenses may be compromised by the fire and because reductions in the insect population due to mortality may be more than compensated by increases in immigration into the burned area (McCullough et al. 1998). Forest fires produce volatiles that are highly attractive to some insect pests and may draw insects from kilometers away (Muona and Rutanen 1994, Holsten et al. 1995, Hart 1998, Schmitz and Blekmann 1998). In particular, some bark beetles show a clear preference for colonizing burned trees (Dixon et al. 1984, Gara et al. 1984, Geiszler et al. 1984, Ehnstrom et al. 1995, Markalas 1991). So in some forest systems, fire can exacerbate damage from forest insects (Geiszler 1980, Gara et al. 1984, Geiszler et al. 1984, Baylis and James 1986, Rasmussen et al. 1996). It is not known why insects are attracted to scorched trees. It may be that they are searching for trees that have been killed outright by the fire and occasionally make mistakes by attacking live trees. It is also possible that fire causes physiological trauma in trees that changes their nutritional quality or limits their defensive responses against attack. Fire damage increases the nutritional quality of lodgepole pine bark for mammals (Jakubas et al. 1994). Any effects of fire

on resin flow in pine trees would be of special significance because resin is the primary defense of pine trees against bark beetles and their associated pathogens (Reeve et al. 1995).

The literature indicates that forest fires can both decrease and increase damage from forest insects. Presumably the outcome depends upon the nature of the fires as well as the species of trees and insect that are involved. It is well known that insects attacks can influence future fires by killing trees and increasing combustible fuels (Geiszler et al. 1980, Wood 1982, Raffa and Berryman 1987).

6.2 METHODS

Response of Itasca bark beetle populations to fire. We used pheromone-baited funnel traps to sample the abundances of *Ips* species and their specialist predators, including *Thanasimus dubius* (Coleoptera: Cleridae) in 23 locations scattered throughout the old growth pine forests of Itasca State Park (Chapter 3). Sampling was conducted in 1997 and again in 1998. Ten sample sites in old growth pine forests were within the prescribed burn conducted in April 1998. Each site was sampled with an array of three traps separated by ~15 m and configured as an equilateral triangle. Within a site, each trap was baited with either ipsdienol + lanierone (produced and preferred by *I. pini*), ipsenol (produced and preferred by *I. grandicollis*), or ipsdienol + ipsenol (produced and preferred by *I. perroti*). Traps were implemented by 1 July in 1997 and 5 May in 1998 and emptied every two weeks through late September in both 1997 and 1998. Pheromone lures were rotated around the array each time the traps were checked to control against spurious effects of trap position. We counted and identified all the *Ips* and *T. dubius* that were captured. Abundance levels were analyzed with an ANOVA model on log transformed data that included burn, date of sampling, burn x date, and site nested in fire.

Effects of prescribed fire on resin flow. We measured the resin flow of 120 mature red pines, 10 trees in each of 12 sites, in August 1997 and July and August 1998 (see Chapter 2 for detailed protocol, description of study sites, and other measurements of the same trees). Two study sites were within the area of the April 1998 prescribed burn. All 10 trees at one site and five trees at the second site were damaged by the fire. Fire damage was assessed as height of highest bark charring (range = 0.35 to 11.54 m, mean ± SE = 4.57 ± 0.91 m). The change in resin flow from 1997 to 1998 was calculated for each tree as Δ Resinflow = $\sqrt{}$Resin98 - $\sqrt{}$Resin97, where $\sqrt{}$Resin98 and $\sqrt{}$Resin97 equal the square root of resin flow (g) in 1997 and 1998. (Square root transformations corrected for mild heteroscedastity of the data and permitted the application of parametric statistics.) Change in resin flow was analyzed with an ANOVA model that included burn, date of sampling in 1998, burn x date of 1998 sampling, crown class, crown class x burn, and burn nested in tree and crown. The relationship between char height and change in resin flow was evaluated with a linear regression.

Effects of experimental scorching on resin flow and beetle attacks. During 1999, we conducted additional experimental studies of the effects of fire on resin flow. We used a large propane torch to burn one side of 40-year-old red pines from a height of 0.5 - 1.5 m on the bole. Within the one meter treatment area, we exposed each of three equally spaced targets to 60 seconds of flame. This treatment had the effect of raising cambium temperatures beneath the bark to about 50 °C and produced scorching damage on the surface of the bark that matched that of many trees within the prescribed burn at Itasca. In most naturally scorched trees, as in our experimental trees, the scorching is largely restricted to one side of the tree (corresponds to the downwind side in a surface forest fire). We measured resin flow of the experimentally scorched trees, and a matched set of control trees, 1 d prior to fire treatment, 3 d after treatment, 9 d after treatment, and 60 d after treatment. Experimental and control trees were intermixed within 1 ha of homogenous, even-aged forest. We also measured the resin flow in 10 red pines that were scorched during May 1999 in a small wildfire in the same forest. Immediately after the fire treatment, we placed pheromone baits (ipsdienol or ipsenol) on 13 of 30 trees within each treatment and began to monitor beetle landings using sticky traps (30 cm of plastic wrap, sprayed with Tanglefoot) wrapped around the circumference of trees at 2 m height. On 25 August 1999, we carefully examined all the study trees to count the number of beetle attacks and evaluate their progress. These studies were conducted at our study sites near Colfax, WI.

6.3 Results and Discussion

Abundance of *Ips* in burned forests. We captured 3697 *I. pini*, 872 *I. grandicollis*, 408 *I. perroti*, and 1759 *T. dubius* in 1998 (Chapter 3, Appendix 4). Compared to unburned sites, the abundance of *I. pini* in burned sites was significantly higher during May of 1998, significantly lower during late July and early August, and no different in September (Fig. 6.1). The abundance of *I. grandicollis* and *I. perroti* was no different between burned and unburned sites. The abundance of *T. dubius* was significantly increased in burned sites, especially during May. Because the fire was conducted prior to the time when most beetles had not emerged from their overwintering sites in the forest litter, the ground fire must have directly killed many insects.

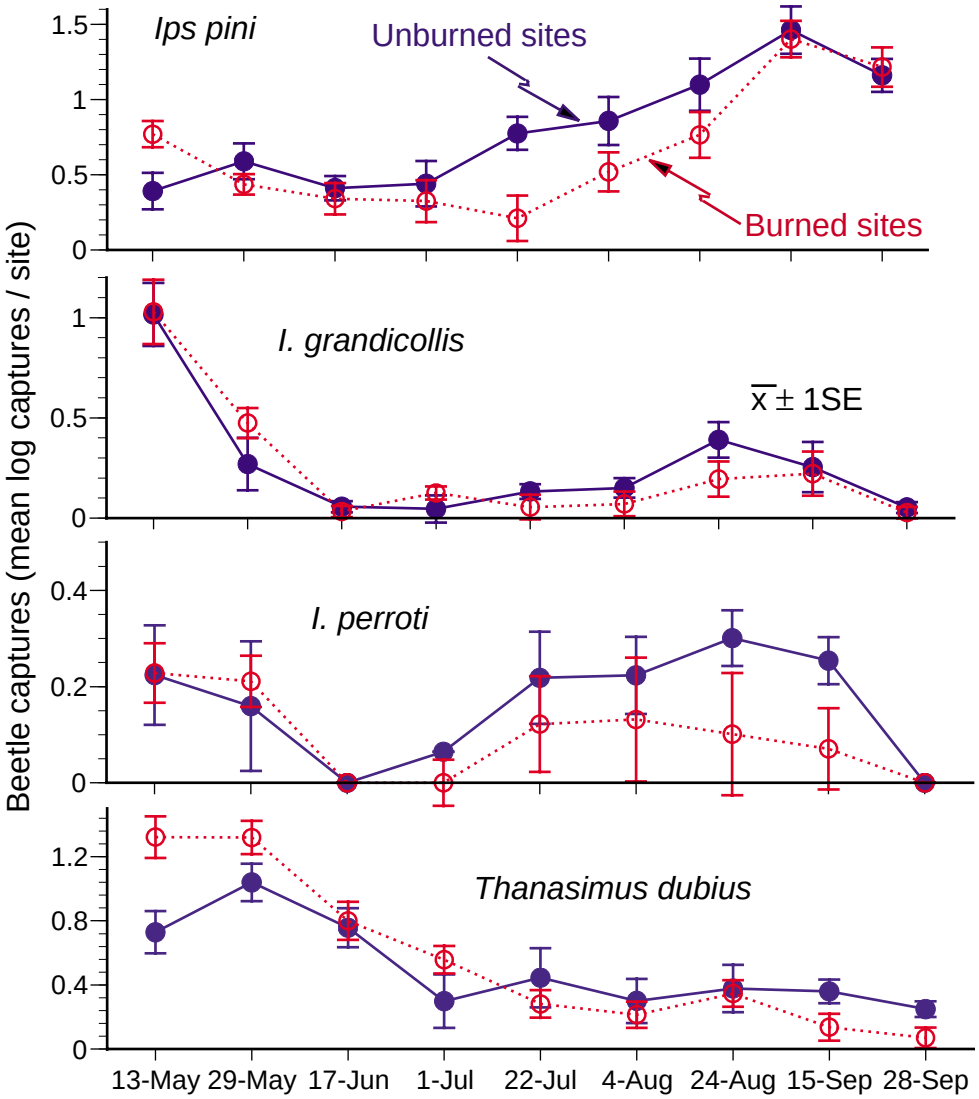


Figure 6.1. Captures during 1998 of bark beetles at sites within old-growth pine forests that were and were not exposed to prescribed fire in April 1998.

The fact that beetle abundance in burned areas increased or remained the same during May implies that there must have been significant immigration of beetles into the burned areas. The temporary decrease in *I. pini* abundance during late July and early August (Fig. 6.1) could have been due to reduced reproductive success of the first generation in burned areas, where they encountered somewhat higher numbers of predators and relatively high resin flow in some of the trees that they attacked. The overall pattern seems to be that fire had only limited and short-term effects on the abundance of bark beetles

Effects of prescribed fire on resin flow. Two to three months after the fire, resin flow was significantly increased in trees that were exposed to fire compared to those that were not (Fig. 6.2; $F_{1, 116} = 6.04$, $P = 0.015$). Trees with low initial resin flow in 1997 showed the greatest increases in resin flow (Fig. 6.2), but there was no effect of crown class (codominant vs intermediate) on the change in resin flow ($F_{1, 116} = 0.43$), nor was there any interaction between crown class and and fire ($F_{1, 116} = 0.28$). Resin flow did not differ between measurements in July and August of 1998. There was a positive relationship between char height (up to 10 m) and change in resin flow ($r^2 = 0.26$, $P = 0.004$).

Effects of experimental scorching on resin flow and beetle attacks. Three days after experimental scorching, resin flow as reduced by about 75% on the scorched side of the tree, with no effect on the unscorched side of the trees (Fig. 6.3, upper middle). Nine days after the fire, resin flow was still reduced by 50% in scorched trees relative to control trees, and the effect was evident on both sides of the scorched trees (Fig. 6.3, upper right). Thirty days after the May wildfire in Colfax, resin flow in scorched trees was almost three-fold higher than in unburned trees (Fig. 6.3, lower left). Sixty days after the experimental scorching, resin flow was about two-fold higher in scorched trees than in control trees (Fig. 6.3, lower right). Bark beetles were much more likely to attack and colonize burned trees than unburned trees (Table 6.1). Nine weeks after the scorching treatment, 11 of 30 burned trees contained *Ips* galleries compared to 0 of 30 control trees (Table 6.1). All of the trees that sustained high attack rates had been baited with a pheromone bubble cap, so presumably the attack rates were higher than they would have been without baiting, but because both burned and unburned trees were baited, it is still clear that the fire treatment increased attack rates. These patterns were also evident at Itasca, where we observed many trees that were rapidly colonized by *Ips* within the scorched area of the lower trunk that was downwind at the time of the prescribed fires in spring of 1998 and 1999 (Fig. 6.4, left).

Feedbacks between fire, bark beetles, and tree mortality. Scorching of the outer bark that accompanies ground fires apparently produces physiological trauma to the inner bark that, for at least 9 d after the fire, compromises the ability of trees to defend themselves by exuding resin from wounds. Presumably bark beetles have evolved the ability to detect fire volatiles, fly to trees that have sustained fire damage, and preferentially attack scorched areas within those trees because their chances for reproductive success are enhanced in trees with reduced resin flow. Recently burned forests are also likely to contain trees that have been completely killed by the fire and have no defenses against beetle attack. However, it appears that bark beetles have only a limited window of opportunity to successfully colonize fire-damaged trees because red pines facultatively increase their resin flow to even higher than baseline levels within 30 d after the fire. This may be an evolved response of red pines to the increased risks of bark beetle attack that accompany fires. In many scorched trees at Itasca and Colfax,

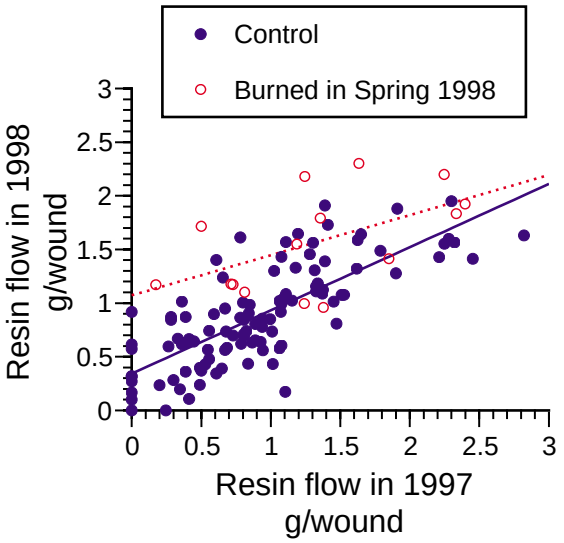


Fig. 6.2. Resin flow in 1998 vs 1997 for mature red pines that were and were not exposed to prescribed fires in the spring of 1998. Trees exposed to fire had significantly elevated resin flow by mid summer of 1998 compared to trees that were not scorched. The difference was especially pronounced in trees that relatively low baseline resin.

copious resin flow in the scorched region of the bole appeared to limit the spatial extent of girdling from bark beetle infestations (Fig. 6.4, right). Some mature red pines that were attacked by beetles following fire damage in the spring of 1998 were still alive in the fall of 1999 and were no longer under attack by beetles (see red pine in Fig. 5.2, lower).

Table 6.1. Number of experimentally burned and unburned trees with bark beetle attacks, oviposition galleries, and surviving *Ips* nine weeks after scorching treatments were applied. Experiment included 60 trees intermixed within a homogenous 1 ha stand of 40-year-old red pine. Half of the trees were experimentally scorched from 0.5 to 1.5 on one side of the bole on 22 June 1999.

Colonization By *Ips*	Unburned trees	Burned trees[a]	
≥1 attack	11	19	
≥5 attacks	2	11	**
Oviposition galleries	0	11	***
Live *Ips* in bark	0	5	**

[a] All attacks were on the burned side of the trees
** $P < .01$; *** $P < .001$; chi-square tests of the null hypothesis that frequencies did not differ between burned and unburned trees.

Nonetheless, scorching and associated beetle damage can result in irreparable loss of vascular connections between the roots and crown. Furthermore, death of the cambium precludes additional growth of wood, phloem, or bark in that region of the bole. The resulting permanent scars are referred to by foresters as “cat-faced scars” (Fig. 6.5, left). These cat-faced scars are very common in the old growth forests at Itasca. In the absence of additional fires, trees can live almost indefinitely even with large cat-faced scars. However, these scars make trees much more sensitive to damage from subsequent fires because the wood is exposed to flames without the benefit of insulation from bark. This makes it more likely that living cambium surrounding cat-faced scars will be traumatized by heat from the fire. This in turn promotes attack of the newly traumatized phloem by bark beetles. After the prescribed burns in 1998 and 1999, we observed many red pines at Itasca that contained new infestations of bark beetles localized within 20 - 50 cm of old cat-faced scars. This results in the death of additional cambium, the loss of insulating bark (in some cases through the action of woodpeckers), an enlargement of the cat-faced scar, and increased vulnerability of the surviving cambium to heat trauma from future fires.

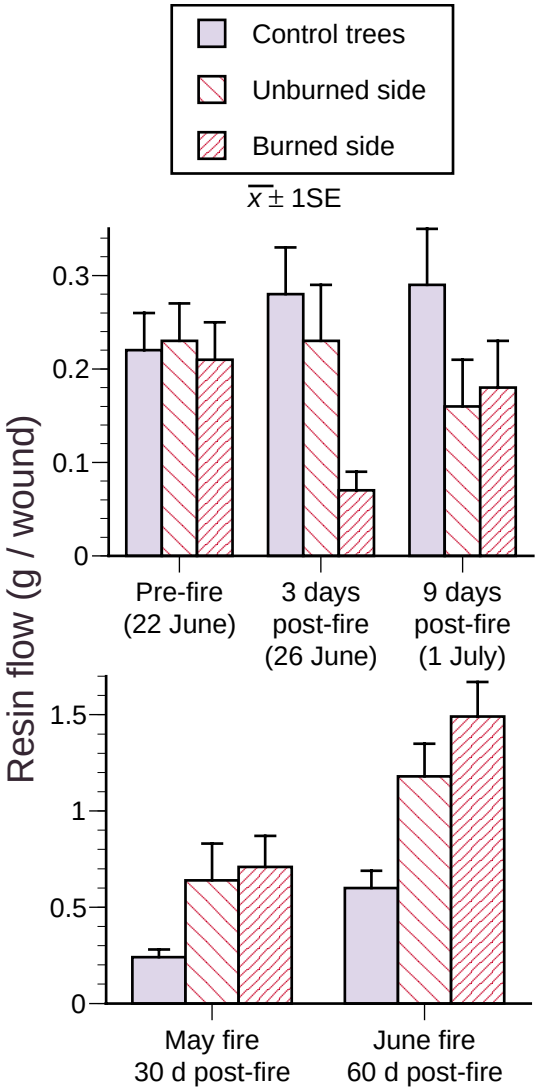


Fig. 6.3. Upper: resin flow in experimentally scorched red pines 1 d before, 3 d after, and 9 d after fire treatments. Lower: resin flow in red pines 30 d after scorching from a natural wildfire and 60 d after experimental scorching.

For images see
http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm

Fig. 6.4. Left: An incipient cat-faced scar forming on a red pine in Itasca that was scorched by prescribed fire during spring 1998. *Ips* bark beetles are colonizing the scorched side of the tree that was on the downwind side of the fire. The attacks are being restricted to this region of the tree by copious resin flow around the periphery of the scorching. Nonetheless, about half the circumference of the tree has been girdled as a result of the fire and beetles. If the tree lives, this damaged area will be evident as a cat-faced scar (Fig. 6.5, left), which will increase the vulnerability of the tree to subsequent fires (Fig. 6.5, right). Right: bark beetle galleries within the phloem of a red pine that was experimentally scorched. The cambium is dead within the infested area, so further tree growth in this region of the bole would be impossible. Note how the phloem has beome impregnated with resin in the region of attack, which appears to have limited the extent of the beetle galleries..

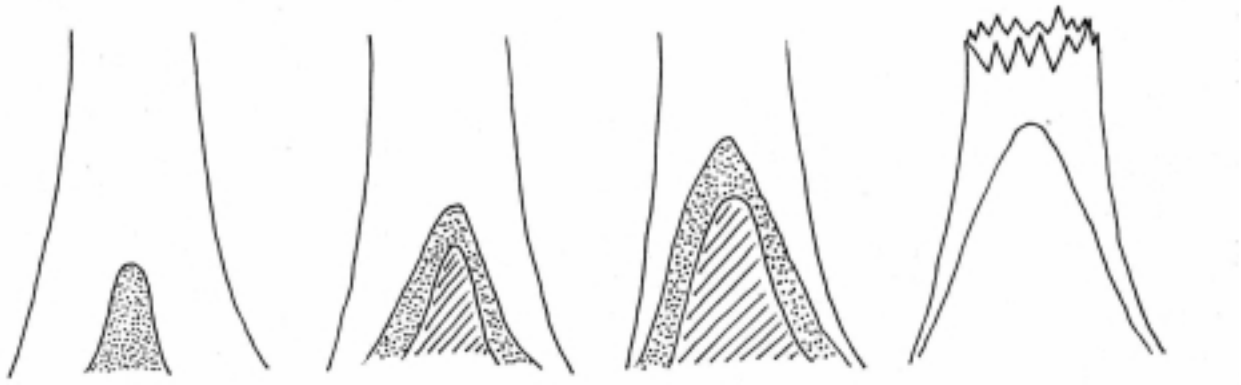
For images see
http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm

Fig. 6.5. Left: Cat-faced scars in mature red pines at Itasca – probably a legacy of past fires and the localized attacks of bark beetles within scorched regions of the bole. In these trees, and many others at Itasca, the cat-faced scars bear evidence of multiple wounding events that were separated by years or decades (probably a sequence of fires followed by beetle attacks). Each wounding event tends to expand the perentage of the trunk that is girdled and increases the amount of wood that is exposed to future fires. Right: one of many trees at Itasca that died from ignition of the exposed wood in a cat-faced scar. This is the endpoint of the positive feedback cycle represented in Fig. 6.7. The downed tree will increase the local fuel load for subsequent fires and increase the probability of fire damage to adjacent trees (Fig. 6.8).

Apparently, this process of sequentially enlarging scars has been important at Itasca within the lifespan of trees that live there now. Examination of the scar tissues in many old trees at Itasca reveal cases where a scar that was initially small has become episodically enlarged at intervals that can be separated by many years. We hypothesize that most of these enlargements can be dated to fires that pre-date the recent era of active fire suppression at Itasca. Enlargement of cat-faced scars increases the probability of catastrophic damage or mortality from future disturbances, especially fires.

The forests at Itasca that were burned in 1998 and 1999 contain many trees that experienced no direct crown damage from the fire but died as a result of surface fire igniting the wood at the site of old cat-faced scars and burning out the inside of the tree (Fig. 6.5, right). This same pattern of high tree mortality from low intensity surface fires igniting old scars has also been reported in old growth forests of *Pinus sylvestris* in Sweden (Linder et al. 1998).

Thus, the interaction of fires and bark beetles can lead to the initiation of scars on the lower bole of red pines (Fig. 6.6, phase I). This initiates a system of positive feedbacks where the scarred tree is increasingly sensitive to damage from future fires, which exposes it to additional attacks by bark beetles, which further increases the sensitivity to future fires (Fig. 6.6, phase II). This process can lead to premature death of the tree when a fire eventually burns out the lower trunk (Fig. 6.6, phase III). Presumably, the average number of fires required to kill a tree after the formation of the initial scar will be greatest if the fires are of low intensity and coincide with times of low bark beetle abundance (Fig. 6.7). There is probably an additional positive feedback because the death of trees from a current fire will tend to increase the risk of scar initiation on nearby trees because a fire-killed tree will tend to (1) increase the abundance of bark beetles that can damage other trees and (2) increase fuel load within the stand, which will increase the heat experienced by nearby trees during present and/or future fires (Fig. 6.8). Because the relationship between fire, bark beetles, and tree mortality appears to involve positive feedbacks (Figs. 6.7 - 6.8), the proportion of trees that succumb to fires would be expected to increase with each additional fire, and it would be easy for forest managers to underestimate the consequences of future fires for tree mortality.



Phase I.
Intiation of fire scar. Combination of fire and bark beetles kills some cambium. Loss of bark reduces insulation against future fires.

Phase II.
Expansion of scar following subsequent fires. Process is allowed by the fire, accelerated by *Ips* bark beetles that invade the newly traumatized phloem surrounding the old fire scar, and limited by inducible increases in resin flow of pine trees following fire.

Phase III.
Tree burns out in a subsequent fire and dies.

Fig. 6.6. A schematic of the process by which fire and beetles interact to produce and enlarge cat-faced scars on the lower trunk of pine trees. These scars can eventually lead to tree mortality when a surface fire ignites the exposed wood and consumes the trunk.

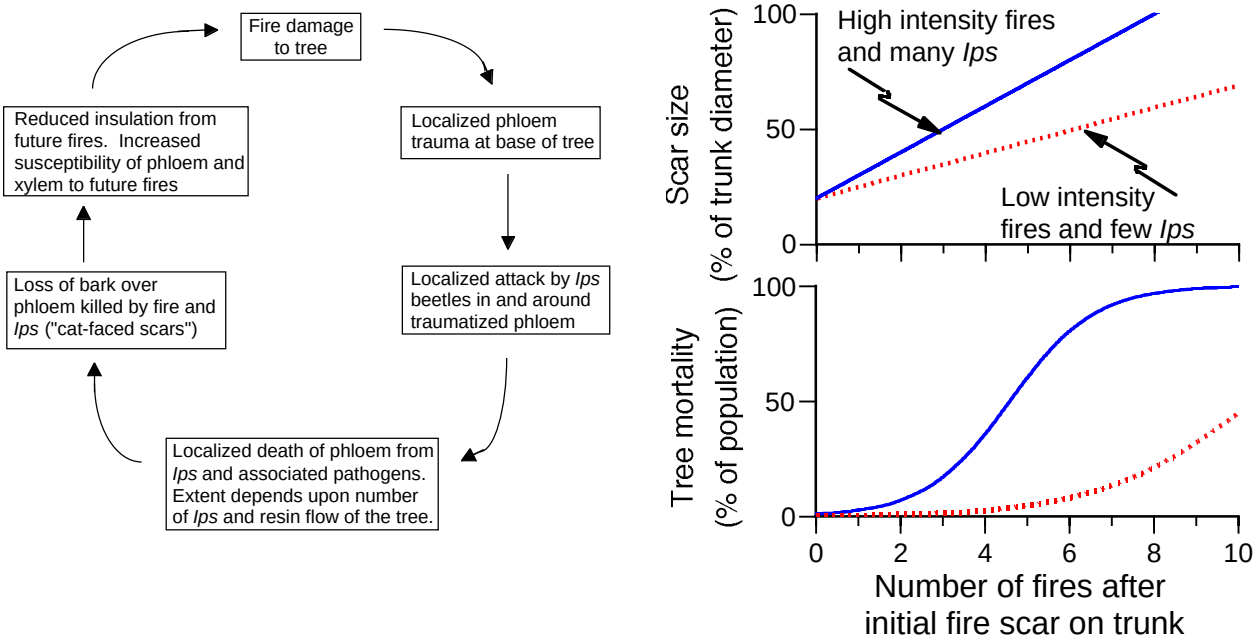


Fig. 6.7. Left: a flowchart of the positive feedback system by which fire and beetles interact to produce and enlarge cat-faced scars on the lower trunk of pine trees. The eventual outcome is for a fire to ignite the exposed wood, consume the trunk, and kill the tree. Right: the number of fire-beetle cycles from initial scar formation until the death of the tree is hypothesized to depend upon fire intensity and the abundance of bark beetles during the weeks immediately following the fire. This positive feedback system creates a risk that tree mortality from prescribed burns will tend to increase with each subsequent burn.

We expanded the simple demographic model from Chapter 5 to evaluate the potential effects of changes in tree mortality rates that might be associated with the interacting effects of prescribed fires and bark beetles on the survivorship of old growth pines in Itasca. With the mortality rates that we used in Chapter 5, a hypothetical pine forest would be reduced to half in about 65 years. It was beyond the scope of this study to develop rigorous estimates of these mortality rates for Itasca, but we used rates that matched our data and intuition for Itasca. Furthermore, a half-life of 65 years seems realistic to us. Prescribed fires will tend to decrease the survivorship of red pine adults at Itasca through (1) the direct effects of killing trees, (2) indirect effects of increasing short term attack rates by bark beetles, and (3) producing scars that increase future susceptibility to fires and beetles. These processes imply an increase in all four parameters that determine mortality rates in Fig. 6.9 (*M1*, *M2*, and *M3*). In the absence of demographic data for mature red pines subjected to surface fires, we can only guess at the magnitude of these increases, but a doubling or tripling of mortality rates does not seem

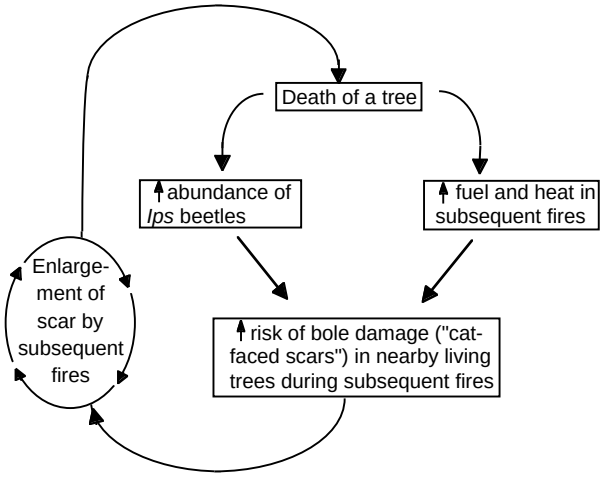


Fig. 6.8. A flowchart of the positive feedback system by which the death of one tree from fire can contribute to the death of nearby trees. When a tree dies, it can provide food that increases the population of bark beetles and fuel that increases the heat of future fires, both of which increase the probability that scars will be initiated on nearby trees. The loop at left is depicted in Figs. 6.6 - 6.7. This positive feedback loop creates a risk that tree mortality from prescribed burns will tend to increase with each subsequent burn.

improbable. For example, if direct mortality from fires of unwounded trees is 10 trees per 1000 and fires are applied every five years, this corresponds to an increase of 2.5 / 1000 in *M1*, as in the middle scenario of Fig. 6.9. Similarly, if fire induces beetle attacks in 50 trees / 1000 (compare to 11 / 30 trees in Table 6.1), and half of them are killed outright (see Chapter 5), then *M2* and *M3* would increase to 10 / 1000, as in the middle scenario of Fig. 6.9.

The model depicted in Fig. 6.9 clearly illustrates that even modest increases in tree mortality rates, which should be expected with the implementation of prescribed fires, could have rather dramatic impacts on the future of old growth forests at Itasca. The model should not be taken as a forecast of tree mortality patterns at Itasca, but as a starting point for the development of models that can guide management decisions by incorporating the processes through which fire and beetles interact to influence tree survival. Demographic models such as these should be refined, parameterized, and evaluated in concert with the development of fire management practices at Itasca. Presumably the optimal fire management strategy is one that carefully balances the costs of reduced survivorship in mature trees against the benefits of possible improvements in red pine regeneration and forest aesthetics.

6.4 MANAGEMENT RECOMMENDATIONS TO MINIMIZE TREE MORTALITY ASSOCIATED WITH PRESCRIBED FIRES

Recommendations that follow from Fig. 6.7.

- Limit fire intensity to minimize the number of new scars that are initiated with each fire.
- Limit fire intensity in areas with scarred trees.
- Increase duration between fires as much as possible, especially in areas with scarred trees.
- Conduct burns when existing scars will be on the upwind side of trees rather than the downwind side of trees.
- Limit intensity and frequency of fires in stands where pine trees have low resin flow.
- Implement a low cost program for monitoring *Ips* population abundance (see Chapter 3) and use these data to:
    - burn in years with relatively low abundance of *Ips* (e.g., following summers of low abundance of *Ips* and winters with high mortality of *Ips*); and
    - burn in park regions where the local abundance of *Ips* is low; avoid areas where the local abundance is high, such as in the vicinity of recent blowdowns.
- Conduct sampling after controlled burns to (1) estimate the probability of new scars, (2) map the location of scarred trees, (3) monitor scar expansion on previously scarred trees, (4) record any tree deaths, (5) estimate the probability of tree death from fire as a function of previous scar size, and (6) map the location of red seedlings and saplings that would be vulnerable to future ground fires.

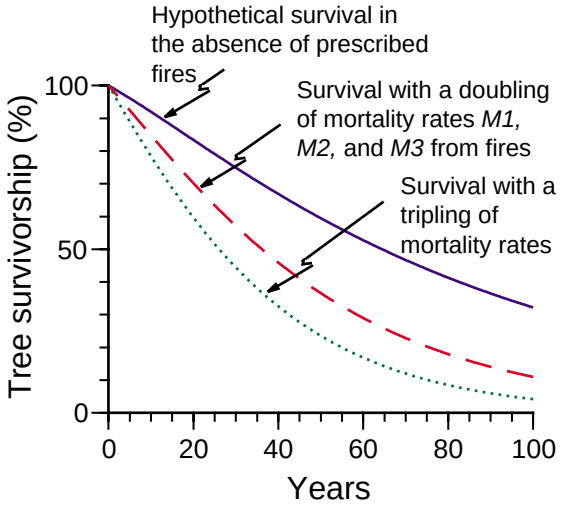


Fig. 6.9. Survivorship curves for a hypothetical population of red pines with annual mortality rates from bark beetles and other causes as estimated in Chapter 5, compared to scenarios with increased mortality rates that might be associated with the interacting effects of prescribed burns and bark beetles. The baseline model assumes constant annual mortality rates in unwounded trees of 5 trees / 1000 from bark beetles (= parameter *M1*) and 2.5 trees / 1000 from other causes (*M2*). The model further assumes that 5 trees / 1000 are wounded from bark beetles or fire per year (*M3*) and that these sustain an annual mortality rate of 50 trees / 1000 (*M4*). With a doubling of *M1*, *M2*, and *M3*, the hypothetical tree population would be reduced to half in 37 years instead of 65 years. With a tripling, it would be reduced to half in 27 years.

Recommendations that follow from Fig. 6.8

- Keep duration between fires long enough to avoid high *Ips* populations from last fire.
- Limit *Ips* increases in trees killed by fires by debarking, flaming, or mass trapping. However, this may have undesirable side effects of reducing the abundance of *Ips* predators and lowering the naturally high biodiversity associated with dead trees, so previous recommendation is preferred except perhaps in cases where there are clusters of downed trees.
- Monitor duration and spatial scale of *Ips* population increases associated with fires in general and downed trees in particular.
- Map the location of downed trees.
- Attempt to limit fire intensity in areas with downed trees.
- Increase duration between fires in areas with downed trees.

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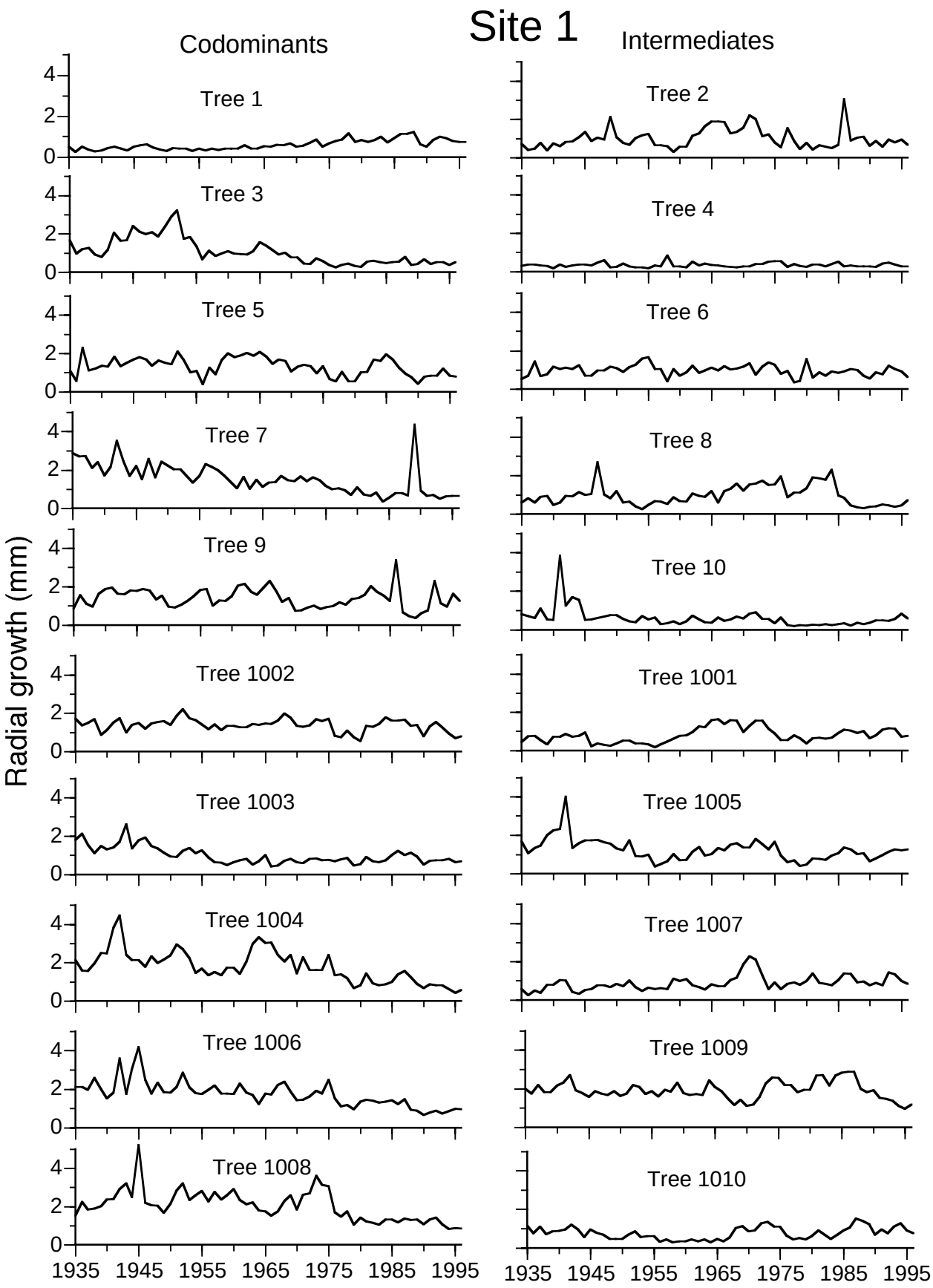
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Tree 3
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Tree 6
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Tree 8
Tree 9
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Tree 1001
Tree 1003
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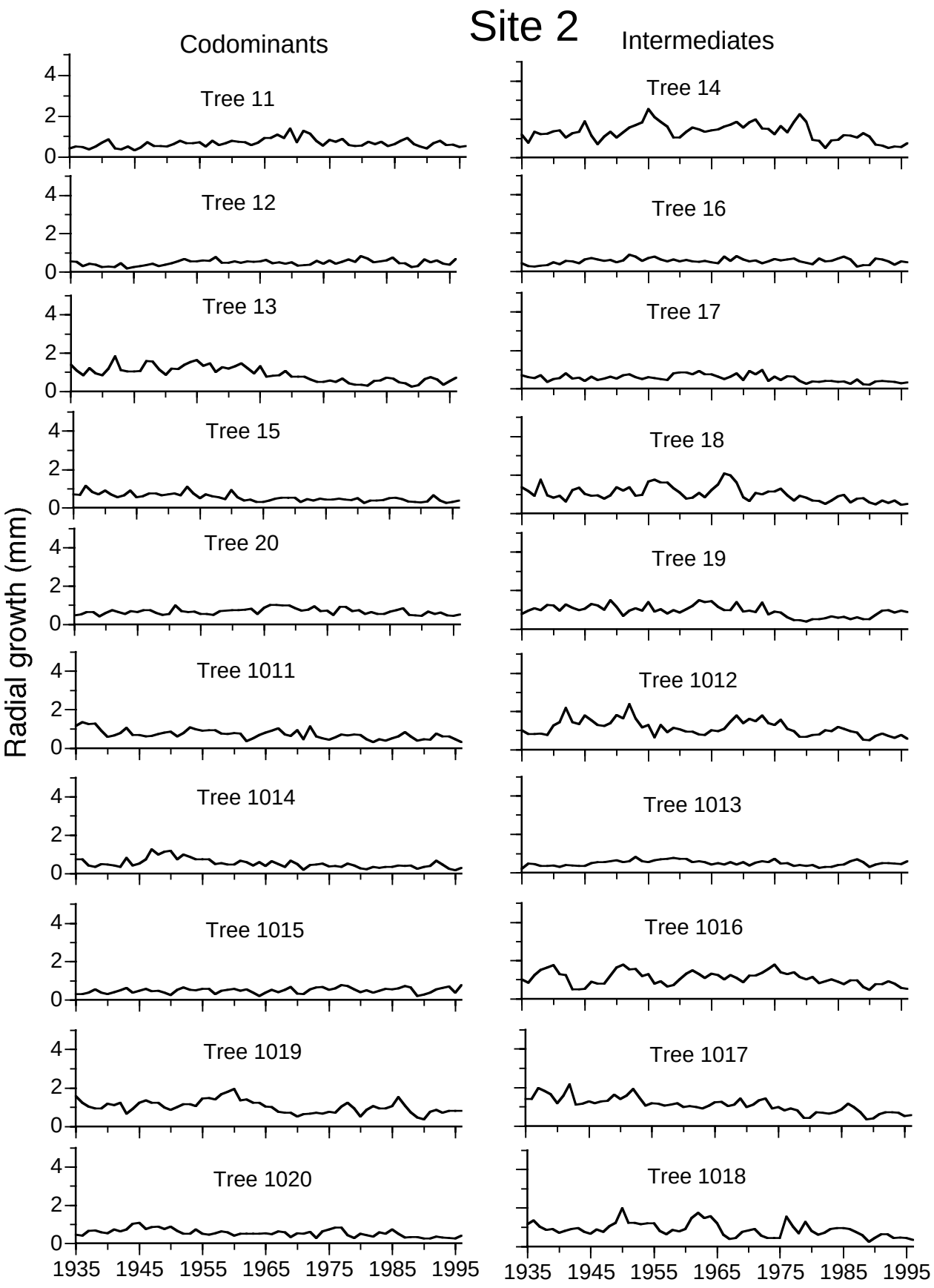
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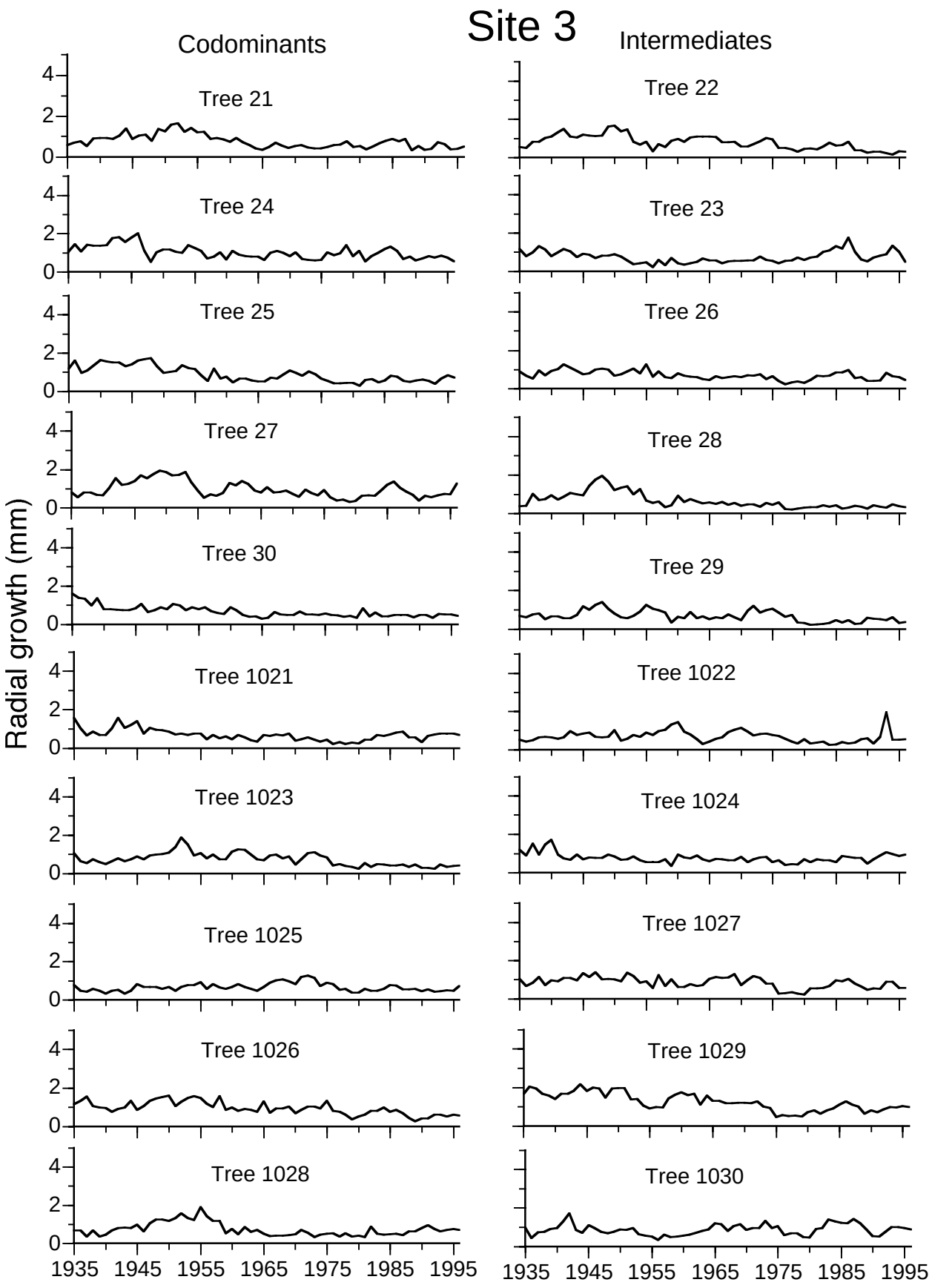
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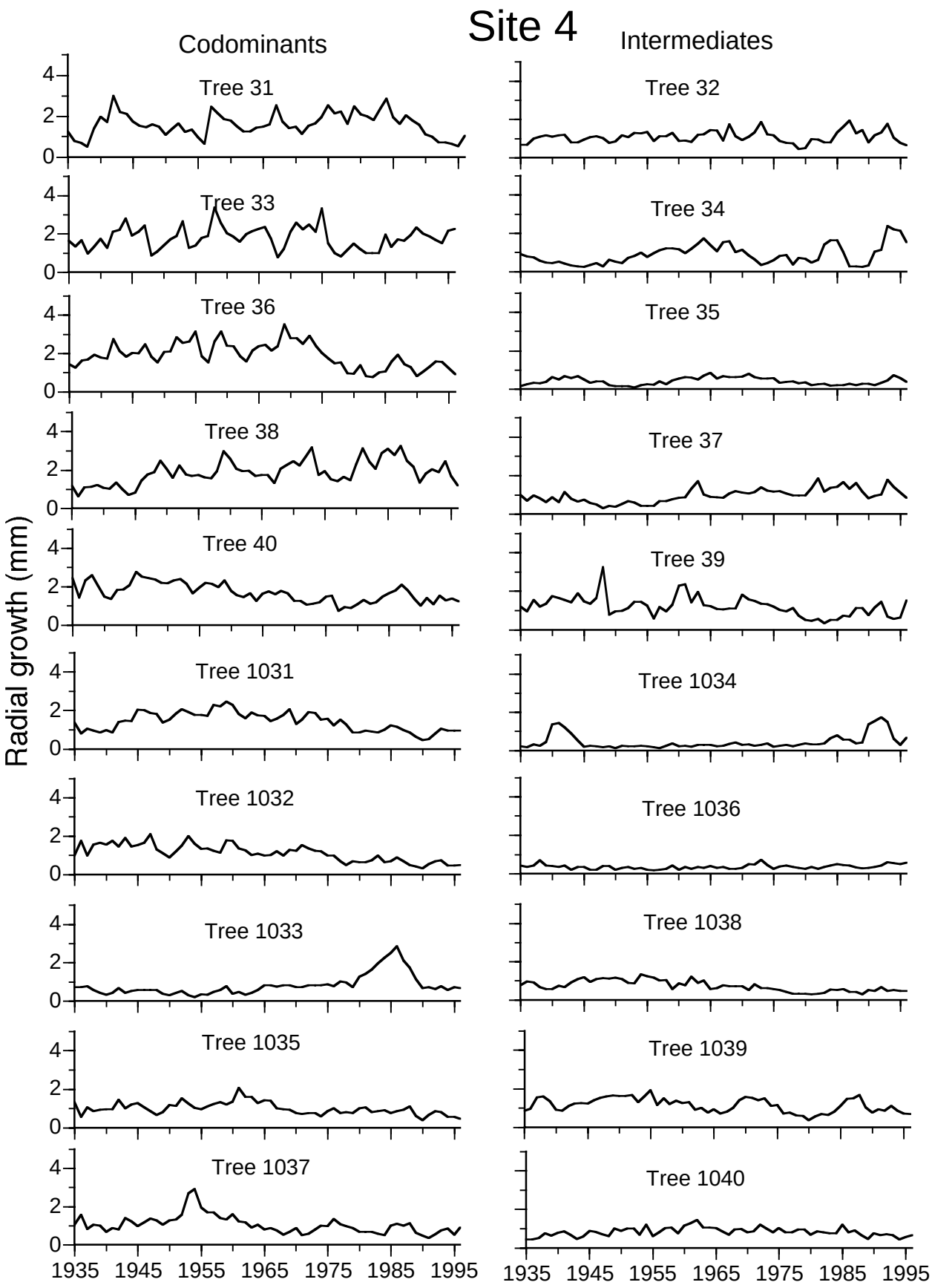
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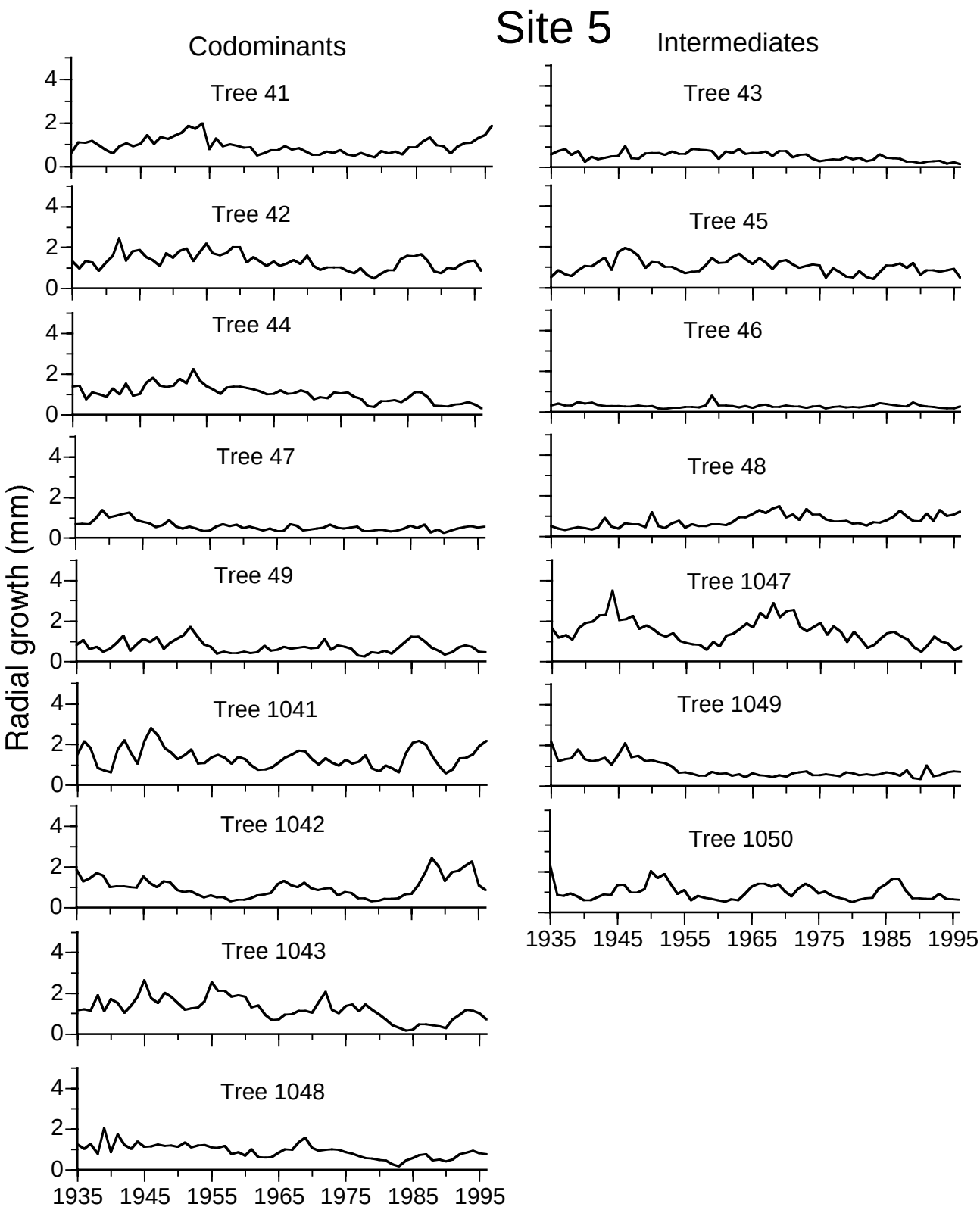
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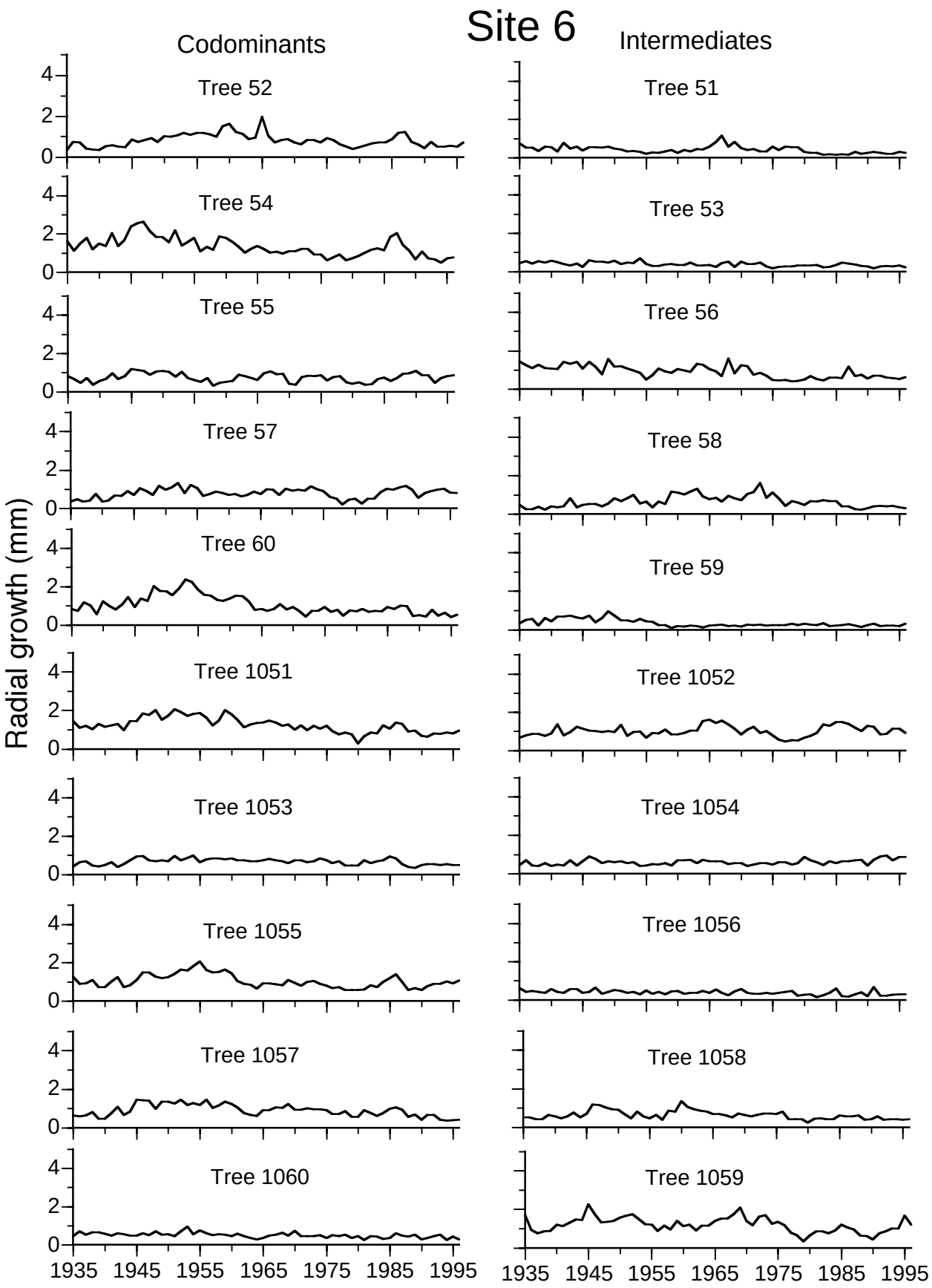
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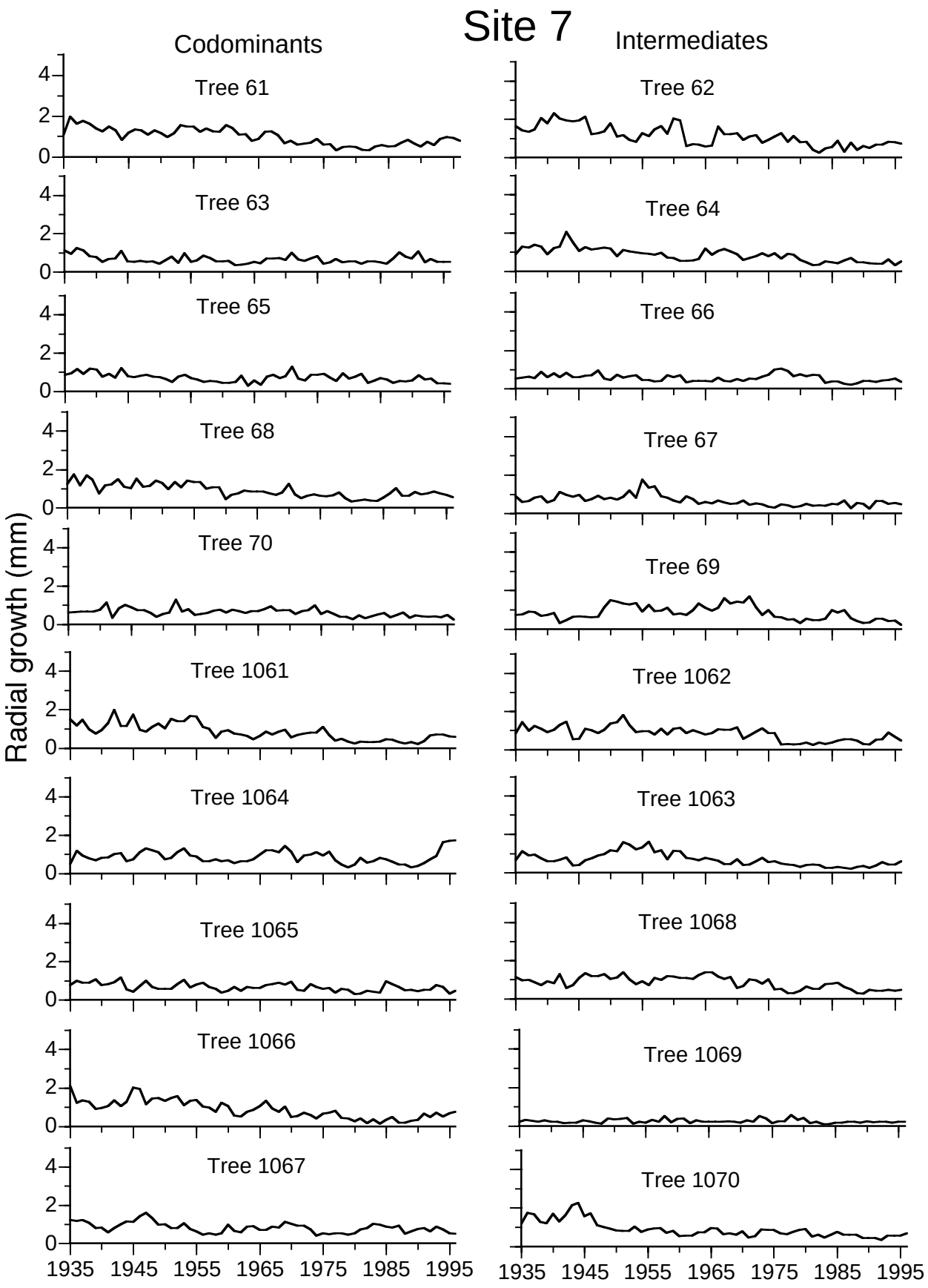
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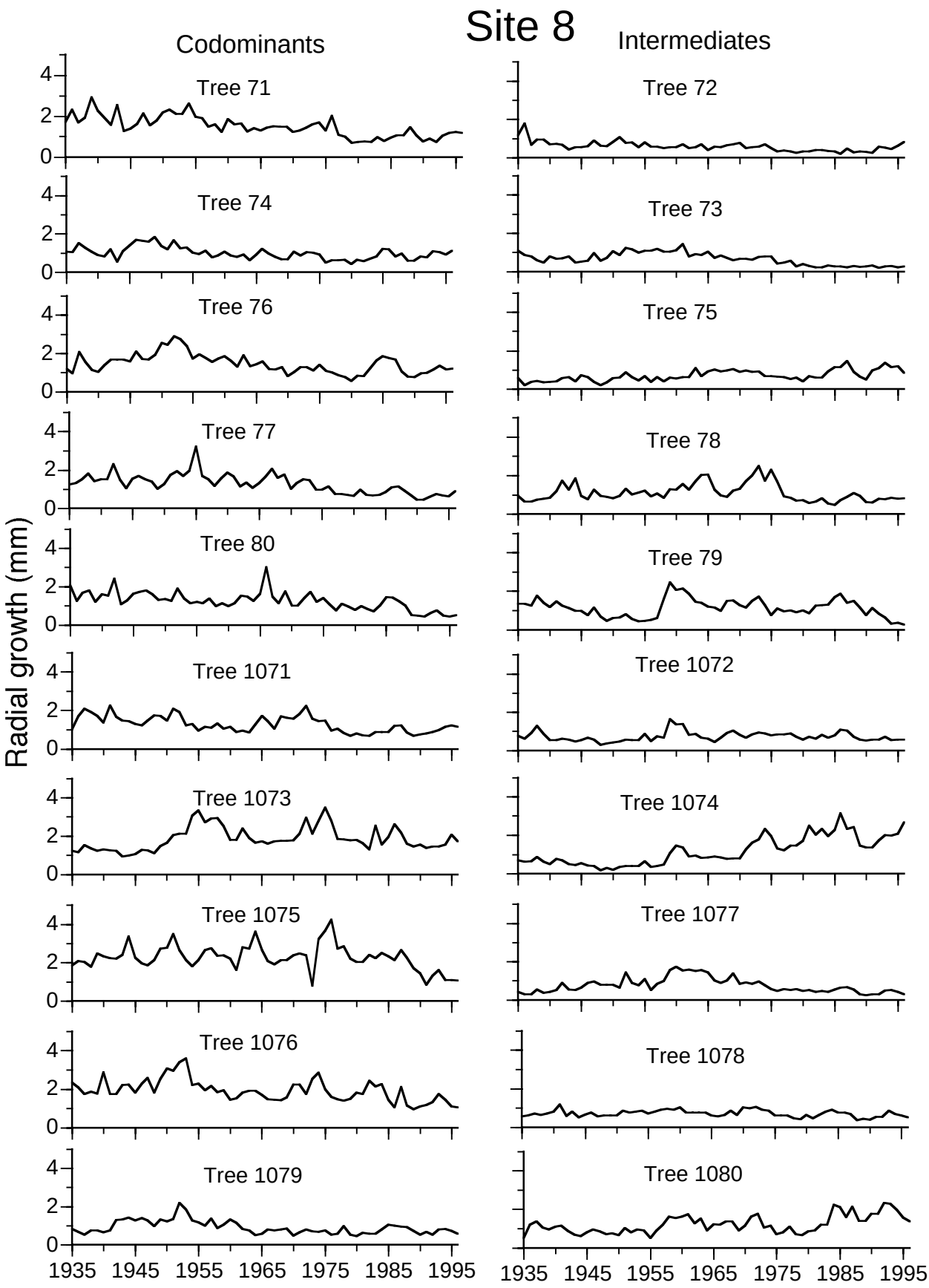
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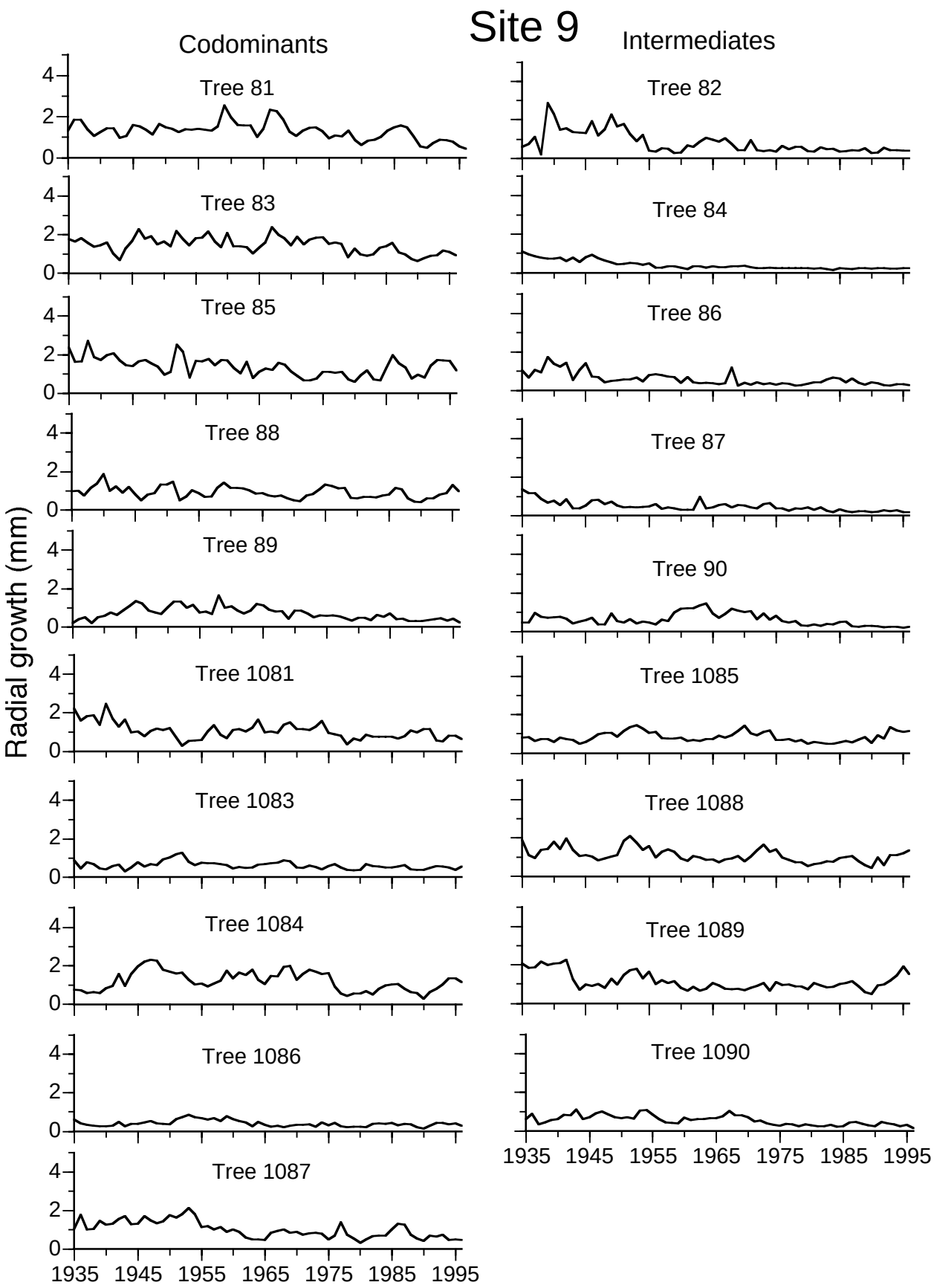
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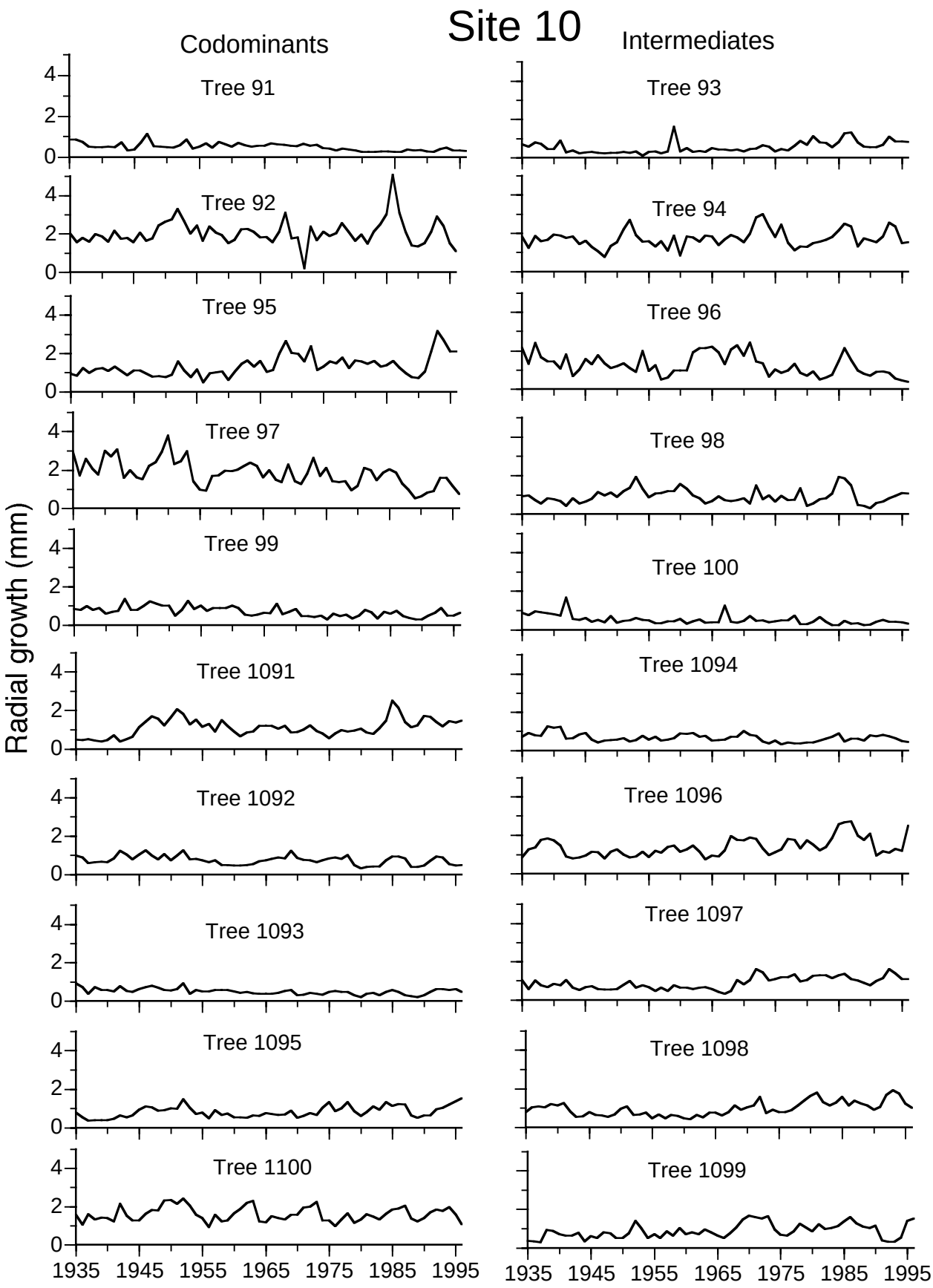
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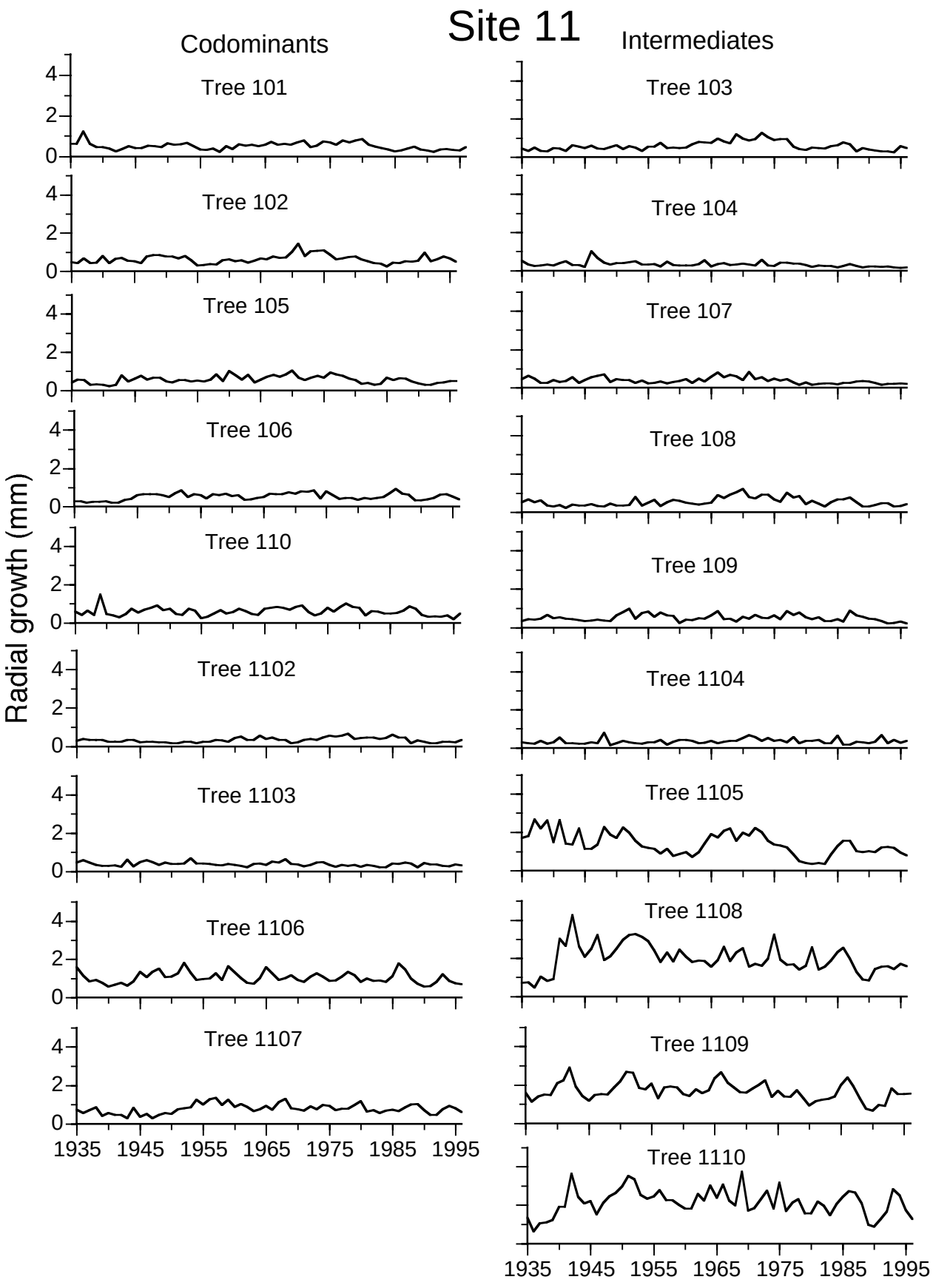
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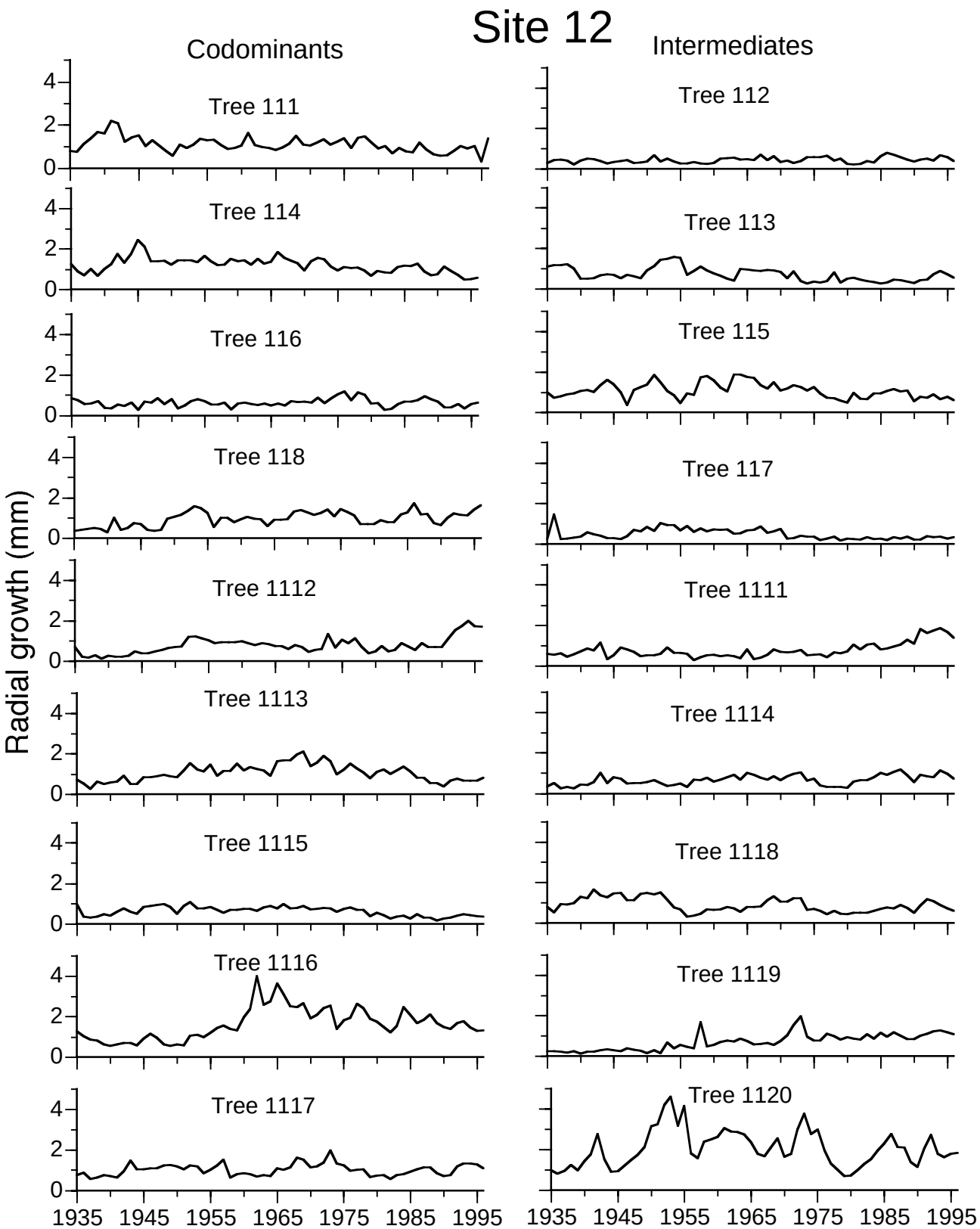
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Site	*Crown*	*Tree*	*Char*	*Start*	*GLI*	*DBH*	*BA*	*Ht*	*%LC*	*Res1*	*Res2*	*Res3*	*Phl1*	*Phl2*	*Phl3*	*Fasc*	*Gr62*	*CV.Gr*	*Gr10*	*Drought*	*Slope*	*%Late*
1	C	1				43	28	28	67	1.13	0.69	1.47	61	48	63	114	0.61	0.40	0.85	0.63	0.0103	
1	C	3				42	41	29	63	0.37	0.09	0.15	66	50	51	114	1.06	0.64	0.52	0.09	-0.0262	
1	C	5				41	48	28	57	0.86	0.38	0.44	86	80	52	115	1.32	0.36	0.87	1.25	-0.0095	
1	C	7				47	32	30	52	3.61	1.48	1.80	66	63	57	119	1.54	0.51	1.06	-0.13	-0.0300	
1	C	9				45	23	29	61	2.72	2.32	3.10	61	47	53	109	1.40	0.38	1.01	2.77	-0.0051	
1	C	1002		1871		50	25	32	58		0.63	0.70		35	72	125	0.76	0.44	1.17	0.82	-0.0053	33.3
1	C	1003		1844		53	25	31	72		0.72	0.57		61	49	125	0.76	0.59	0.79	0.71	-0.0160	36.5
1	C	1004				61	18	46	79		2.04	1.85		32	70	120	0.64	1.30	0.85	0.73	-0.0301	35.3
1	C	1006				63	23	29	74		2.93	1.91		49	68	136	0.75	0.88	0.91	0.58	-0.0264	32.8
1	C	1008				60	25	31	62		1.63	2.17		50	76	125	1.41	0.57	1.15	0.10	-0.0255	34.3
1	I	2				33	25	25	59	0.00	0.40	0.00	68	43	54	123	1.01	0.52	0.85	2.41	0.0025	
1	I	4				24	37	22	61	0.31	0.37	0.12	40	43	35	112	0.34	0.35	0.32	-0.03	0.0002	
1	I	6				26	46	28	53	1.22	0.03	0.03	51	58	51	115	0.97	0.29	0.88	0.37	-0.0023	
1	I	8				27	28	25	75	0.13	0.68	1.45	46	46	47	120	0.97	0.54	0.43	0.46	0.0015	
1	I	10				25	30	17	54	0.13	0.37	0.40	57	47	45	103	0.60	0.85	0.46	-0.04	-0.0118	
1	I	1001		1871		29	25	26	63		0.08	0.20		34	48	121	0.68	0.57	0.93	0.46	0.0077	34.5
1	I	1005		1877		41	28	28	71		0.21	0.24		48	56	123	1.54	0.37	1.06	0.72	-0.0140	44.4
1	I	1007		1845		28	25	24	61		0.41	0.43		38	47	117	0.81	0.47	1.03	0.63	0.0093	38.4
1	I	1009		1863		42	34	26	67		0.34	0.61		59	66	117	1.30	0.36	1.62	0.98	-0.0006	33.9
1	I	1010		1841		33	25	25	66		0.36	0.23		32	49	109	0.76	0.42	1.05	0.37	0.0038	40.2
2	C	11			45	66	16	31	61	4.89	0.36	5.11	75	50	63		0.68	0.31	0.61	0.39	0.0027	
2	C	12	0.8		46	66	25	38	74	5.45	1.21	6.60	58	43	64		0.48	0.29	0.47	0.42	0.0029	
2	C	13	0.5		37	85	25	31	61	5.75	1.72	6.44	51	48	50		0.91	0.43	0.51	0.33	-0.0161	
2	C	15	1.6		46	71	37	32	39	5.05	7.46	2.78	60	40	42	127	0.54	0.37	0.36	0.27	-0.0082	
2	C	20				68	16	34	65	1.15	0.87	0.82	64	48	61		0.67	0.24	0.55	0.28		
2	C	1011				62	30	35	36		0.52			41	48	144	0.50	0.48	0.54	0.13	-0.0083	30.2
2	C	1014				62	44	48	70		2.23	1.17		40	43	116	0.47	0.51	0.36	0.06	-0.0073	32.9
2	C	1015				61	44	33	67		0.51	1.52		44	51	135	0.66	0.21	0.52	0.36	0.0023	34.9
2	C	1019		1832		53	28	26	58		5.82	4.27		40	44	121	0.76	0.44	0.73	1.19	-0.0081	33.5
2	C	1020				58	16	30	41		1.10	0.86		.	37	111	0.30	0.64	0.32	0.26	-0.0060	36.3
2	I	14				42	34	27	43	7.96	0.83	5.53	57	38	58		1.32	0.33	0.83	0.07	-0.0069	
2	I	16				59	39	29	69	0.88	1.19	0.22	52	43	44		0.54	0.26	0.47	0.42	0.0006	
2	I	17				61	28	34	63	3.20	0.67	4.66	57	66	46		0.55	0.34	0.33	0.16	-0.0047	
2	I	18	0.7			38	34	28	64	1.54	0.90	1.09	62	58	46		1.01	0.38	0.59	0.41	-0.0096	
2	I	19	0.4			27	28	29	50	0.53	1.99	0.88	58	45	49		0.93	0.31	0.74	0.13	-0.0086	
2	I	1012		1846		46	23	32	54		1.54	1.25		50	62	136	0.42	0.96	0.72	0.61	-0.0097	38.1
2	I	1013		1775		48	37	30	72		1.90	0.49		45	65	138	0.42	0.33	0.51	0.14	0.0000	40.4
2	I	1016		1840		36	28	25	63		4.94	4.76		46	53	115	0.80	0.43	0.74	0.30	-0.0056	42.2
2	I	1017		1843		41	39	27	59		0.98	1.16		39	51	126	0.75	0.53	0.62	0.76	-0.0175	36.9
2	I	1018		1827		36	41	34	60		0.25	0.09		44	55	109	0.25	1.45	0.49	0.45	-0.0088	38.6
3	C	21			38	45	44	23	69	0.79	0.51	0.36	56	38	49	114	0.76	0.42	0.51	0.42	-0.0101	
3	C	24				52	44	27	78	1.16	1.03	0.95	60	44	52	125	1.02	0.33	0.76	0.71	-0.0109	
3	C	25			38	39	41	25	37	0.68	0.61	0.49	50	70	58	100	0.89	0.44	0.62	0.21	-0.0165	
3	C	27				31	37	25	37	0.62	0.33	0.45	74	37	53	94	0.96	0.44	0.75	0.97	-0.0098	
3	C	30				40	57	27	67	0.46	0.70	0.40	71	28	47	125	0.66	0.42	0.46	0.00	-0.0117	
3	C	1021		1831		52	39	27	59		1.58	1.80		66	52	141	0.72	0.40	0.65	0.50	-0.0085	32.3
3	C	1023				51	37	28	57		0.41	0.56		39	48	115	0.51	0.66	0.37	0.14	-0.0102	37.1

Site	*Crown*	*Tree*	*Char*	*Start*	*GLI*	*DBH*	*BA*	*Ht*	*%LC*	*Res1*	*Res2*	*Res3*	*Phl1*	*Phl2*	*Phl3*	*Fasc*	*Gr62*	*CV.Gr*	*Gr10*	*Drought*	*Slope*	*%Late*
3	C	1025				44	34	28	71		0.51	0.72		43	55	128	0.79	0.27	0.52	0.30	0.0002	36.5
3	C	1026		1840		46	30	27	54		0.37	0.51		58	44	124	0.55	0.61	0.50	0.42	-0.0130	28.0
3	C	1028				44	39	27	65		0.69	0.44		44	41	125	0.97	0.35	0.70	-0.28	-0.0061	32.0
3	I	22			35	26	41	19	45	0.06	0.00	0.00	60	71	37	109	0.79	0.46	0.35	0.41	-0.0136	
3	I	23				24	39	24	60	0.00	0.16	0.06	49	40	42	117	0.75	0.40	0.92	0.68	0.0001	
3	I	26			39	37	34	30	75	0.47	0.40	0.29	53	58	43	116	0.70	0.33	0.59	0.44	-0.0070	
3	I	28			36	32	37	26	69	0.09	0.03	0.17	69	56	30	115	0.64	0.63	0.35	-0.01	-0.0145	
3	I	29				29	51	29	43	0.17	0.43	0.46	62	63	59	112	0.66	0.42	0.44	-0.23	-0.0074	
3	I	1022		1855		32	14	27	74		0.26	0.04		58	40	120	0.46	0.66	0.64	-0.18	-0.0027	38.4
3	I	1024		1843		29	34	27	72		0.23	0.22		51	40	127	0.68	0.36	0.82	0.38	-0.0050	37.6
3	I	1027		1833		32	46	15	54		0.19	0.06		58	56	122	0.72	0.40	0.70	0.46	-0.0077	39.2
3	I	1029		1848		41	23	19	76		0.58	0.45		47	52	124	1.14	0.40	0.91	0.48	-0.0195	39.5
3	I	1030		1831		31	32	24	63		0.61	0.24		47	61	128	0.84	0.33	0.91	0.64	0.0022	39.8
4	C	31			42	45	39	28	59	1.99	2.34	3.73	59	65	46	122	1.59	0.36	1.12	0.50	0.0005	
4	C	33				38	28	27	58	0.61	0.76	0.74	65	41	52	114	1.79	0.32	1.91	-1.01	-0.0005	
4	C	36				44	34	29	64	1.05	2.03	1.38	53	44	60	111	1.89	0.34	1.31	0.79	-0.0144	
4	C	38				38	18	28	66	1.93	4.76	2.69	70	53	61	127	1.88	0.33	2.03	1.45	0.0183	
4	C	40				46	37	29	35	0.20	0.12	0.88	67	37	48	93	1.68	0.29	1.42	0.82	-0.0178	
4	C	1031		1904		36	46	29	65		0.13	0.03		48	57	130	0.80	0.61	0.81	0.68	-0.0112	38.8
4	C	1032		1903		43	34	28	72		0.74	0.71		43	37	122	0.42	1.06	0.53	0.55	-0.0193	40.6
4	C	1033		1897		39	37	31	63		0.84	1.41		44	50	130	0.64	0.86	0.97	2.17	0.0163	39.8
4	C	1035		1896		35	37	37	69		0.34	0.03		53	56	125	0.51	0.62	0.69	0.46	-0.0076	45.2
4	C	1037		1897		40	34	33	71		1.89	0.70		46	42	130	0.56	0.84	0.73	0.62	-0.0116	38.1
4	I	32			42	29	32	27	61	0.99	1.23	0.35	56	38	52	106	1.09	0.29	1.21	0.82	0.0025	
4	I	34			44	22	28	22	43	0.35	0.71	0.91	60	35	39	124	0.89	0.58	1.15	0.67	0.0116	
4	I	35				17	32	19	64	0.17	0.00	0.05	49	49	37	117	0.41	0.45	0.38	-0.08	-0.0003	
4	I	37			40	26	44	26	66	0.45	0.41	0.24	63	51	66	128	0.96	0.38	1.19	0.83	0.0127	
4	I	39			36	35	34	33	76	0.15	0.77	0.75	66	52	32	133	1.20	0.42	0.96	-0.03	-0.0128	
4	I	1034		1899		23	30	18	63		0.03	0.00		55	50	136	1.42	0.28	0.91	-0.77	0.0056	42.4
4	I	1036		1904		27	34	26	50		0.28	0.22		50	39	121	0.50	0.23	0.43	0.17	0.0015	47.0
4	I	1038		1897		23	39	35	76		0.05	0.40		49	37	127	0.51	0.55	0.47	0.08	-0.0107	43.3
4	I	1039				29	28	29	46		0.67	0.08		40	49	113	0.84	0.43	1.01	0.72	-0.0086	35.3
4	I	1040		1901		20	32	16	65		0.11	0.00		41	47	120	0.88	0.25	0.64	0.04	0.0003	37.1
5	C	41	3.4		39	75	9	32	61	1.55	4.84	4.68	66	54	68	107	0.95	0.39	1.14	0.56	-0.0032	
5	C	42	1.3		61	55	18	34	68	3.42	1.04	3.28	53	35	63	130	1.31	0.31	1.12	0.84	-0.0103	
5	C	44	6.4			43	39	35	68	1.84	3.49	2.95	50	44	43	130	1.04	0.38	0.57	0.68	-0.0152	
5	C	47	6.3			50	34	30	50	0.25	3.81	2.19	38	39	37		0.58	0.41	0.47	0.26	-0.0081	
5	C	49	6.9			49	30	33	74	2.67	5.04	5.57	59	49	46	121	0.73	0.40	0.62	0.89	-0.0049	
5	C	50	7.1		36	44	30	29	69	1.41	2.47	2.34	51	66	50	134	1.01	0.39	0.80	0.72	-0.0062	
5	C	1041				65	11	32	63		0.95	1.90		66	67	122	2.05	0.24	1.39	1.58	-0.0047	24.7
5	C	1043				48	14	40	67		3.03	1.65		67	44	140	0.98	0.57	0.73	0.18	-0.0188	32.4
5	C	1044				60	16	26	52		1.28	2.31		34	47	142						
5	C	1046				70	32	31	62		9.72	7.77		44	48	141						
5	C	1048				51	30	34	62		0.44	0.48		47	52	153	0.92	0.38	0.68	0.30	-0.0129	22.4
5	I	43	11.5		51	38	39	37	59	0.03	1.06	1.72	46	35	35	114	0.53	0.41	0.24	0.25	-0.0070	
5	I	45	7.0		29	41	39	28	58	0.51	0.74	2.24	64	50	36	109	1.02	0.34	0.87	0.45	-0.0057	
5	I	46	7.0			36	37	33	51	1.90	1.07	0.79	67	48	44	128	0.28	0.36	0.26	0.05	-0.0012	

Site	*Crown*	*Tree*	*Char*	*Start*	*GLI*	*DBH*	*BA*	*Ht*	*%LC*	*Res1*	*Res2*	*Res3*	*Phl1*	*Phl2*	*Phl3*	*Fasc*	*Gr62*	*CV.Gr*	*Gr10*	*Drought*	*Slope*	*%Late*
5	I	48	7.6		42	34	34	28	64	0.66	1.31	1.12	56	37	46	110	0.77	0.39	1.01	0.23	0.0098	
5	I	1042				39	14	29	64		0.69	0.85		36	48	138	0.80	0.64	1.73	-0.22	0.0023	33.5
5	I	1045				38	25	25	63		0.58	0.61		46	38	135						
5	I	1047				40	25	30	59		2.54	3.07		41	50	134	0.85	0.72	0.88	0.97	-0.0135	32.5
5	I	1049				42	9	19	61		3.22	2.94		37	39	138	0.73	0.58	0.61	0.29	-0.0168	26.9
5	I	1050				46	14	25	63		0.80			42	50	133	0.93	0.43	0.83	0.94	-0.0043	27.2
6	C	52				52	60	31	55	0.71	1.03	0.64	68	54	46	115	0.82	0.39	0.66	0.75	-0.0011	
6	C	54				52	39	32	73	0.64	0.72	1.36	55	63	68	126	1.32	0.37	0.97	1.14	-0.0169	
6	C	55			39	46	57	35	59	0.79	0.91	0.44	69	46	48	115	0.75	0.30	0.84	-0.50	-0.0010	
6	C	57				50	46	28	50	0.75	0.37	0.44	75	46	52	128	0.79	0.33	0.91	0.44	0.0024	
6	C	60				62	34	31	46	6.02	2.26	1.75	77	44	55	120	1.04	0.45	0.63	0.32	-0.0141	
6	C	1051				54	39	30	63		0.16	0.68		66	58	125	0.80	0.49	0.87	0.69	-0.0132	36.2
6	C	1053				53	55	33	68		0.46	0.41		53	57	118	0.51	0.31	0.50	0.34	-0.0020	38.5
6	C	1055				57	39	37	64		0.49	0.55		46	55	116	1.02	0.34	0.83	0.84	-0.0076	36.4
6	C	1057		1825		51	37	36	71		0.49	0.44		40	42	139	0.38	0.81	0.54	0.64	-0.0069	38.4
6	C	1060				65	30	28	58		0.00	0.00		79	54	132	0.33	0.39	0.41	0.32	-0.0039	35.6
6	I	51				24	60	24	48	0.04	0.06	0.05	51	50	39	112	0.42	0.46	0.24	-0.07	-0.0049	
6	I	53			32	34	69	32	62	0.00	0.13	0.04	53	67	45	128	0.38	0.30	0.30	0.19	-0.0037	
6	I	56			27	38	28	25	60	0.11	0.37	0.53	65	47	48	126	0.90	0.36	0.69	0.02	-0.0125	
6	I	58			34	34	30	32	64	1.33	0.75	1.40	74	55	61	115	0.63	0.48	0.34	0.09	0.0003	
6	I	59				26	28	22	38	0.00	0.28	0.49	51	50	37	121	0.34	0.57	0.22	0.00	-0.0067	
6	I	1052		1837		42	37	29	72		0.42	0.58		36	44	128	0.75	0.36	1.11	0.18	0.0024	37.4
6	I	1054		1834		39	46	28	62		0.15	0.41		44	47	119	0.72	0.19	0.74	0.21	0.0030	38.9
6	I	1056				38	44	33	68		0.11	0.06		48	49	114	0.25	0.48	0.30	0.00	-0.0034	37.2
6	I	1058				34	53	29	56		0.14	0.67		55	41	124	0.36	0.62	0.45	0.13	-0.0046	40.6
6	I	1059		1848		42	32	25	57		0.42	0.59		48	53	115	1.10	0.35	0.90	0.64	-0.0082	35.5
7	C	61			32	51	18	29	71	1.76	0.96	1.53	60	52	51	99	1.00	0.40	0.77	0.02	-0.0170	
7	C	63				47	16	28	67	1.89	1.29	1.24	51	41	40	122	0.66	0.31	0.70	-0.27	-0.0034	
7	C	65				50	18	30	63	3.65	5.29	2.13	53	57	43	94	0.71	0.31	0.54	0.05	-0.0055	
7	C	68				47	18	30	70	2.64	2.68	2.37	55	64	59	86	0.91	0.39	0.74	-0.09	-0.0147	
7	C	70				42	30	30	61	1.73	1.24	2.26	43	49	41	112	0.62	0.33	0.42	-0.09	-0.0062	
7	C	1061				56	9	30	66		2.29	3.49		49	47	130	0.49	0.87	0.47	0.20	-0.0177	37.1
7	C	1064		1825		55	7	32	74		0.77	0.66		68	48	136	1.87	0.17	0.89	0.24	-0.0010	34.9
7	C	1065		1822		50	9	27	68		0.21	0.24		60	41	127	0.47	0.44	0.54	0.37	-0.0058	34.2
7	C	1066				57	18	31	63		4.62	2.96		33	48	119	0.89	0.53	0.48	0.15	-0.0204	35.4
7	C	1067				53	25	33	67		0.62	0.47		61	52	127	0.42	0.61	0.69	0.08	-0.0067	38.5
7	I	62			56	44	9	27	64	0.88	0.79	0.68	43	34	43	113	1.14	0.45	0.63	0.27	-0.0215	
7	I	64			50	42	11	22	60	1.93	2.27	1.62	28	53	36	120	0.85	0.40	0.49	-0.06	-0.0149	
7	I	66			49	43	14	30	66	0.37	3.78	0.74	35	34	51	114	0.56	0.34	0.37	-0.03	-0.0035	
7	I	67				25	18	21	65	0.24	0.23	0.00	37	26	39	116	0.66	0.42	0.50	0.00	-0.0091	
7	I	69			55	37	23	29	55	1.76	1.85	0.91	38	58	32	111	0.83	0.44	0.46	0.54	-0.0061	
7	I	1062		1824		45	9	27	45		5.23	3.07		48	40	116	0.38	0.94	0.52	0.17	-0.0137	37.5
7	I	1063		1822		45	21	30	64		2.16	1.90		53	52	111	0.55	0.63	0.37	-0.04	-0.0114	32.8
7	I	1068				37	21	31	62		0.42	0.30		42	49	127	0.51	0.64	0.44	0.55	-0.0114	40.8
7	I	1069		1830		36	28	29	52		0.80	0.38		40	27	111	0.09	1.17	0.21	-0.09	-0.0005	36.0
7	I	1070				36	21	30	65		1.21	1.83		51	36	124	0.72	0.59	0.51	0.17	-0.0176	40.6
8	C	71			47	40	39	26	76	2.28	1.09	1.23	57	51	58	120	1.50	0.34	1.07	0.30	-0.0212	

Site	Crown	Tree	Char	Start	GLI	DBH	BA	Ht	%LC	Res1	Res2	Res3	Phl1	Phl2	Phl3	Fasc	Gr62	CV.Gr	Gr10	Drought	Slope	%Late
8	C	74				38	39	24	68	1.19	1.52	0.73	72	38	57	119	0.99	0.32	0.89	0.57	-0.0083	
8	C	76				41	30	26	73	1.39	2.53	1.14	75	51	59	126	1.46	0.35	1.12	1.00	-0.0133	
8	C	77			37	46	28	26	71	0.89	1.25	0.00	71	45	62	119	1.28	0.39	0.72	0.62	-0.0182	
8	C	80				41	30	26	64	1.23	1.92	0.61	70	47	64	123	1.25	0.38	0.65	0.93	-0.0162	
8	C	1071		1895		37	44	24	78		1.18	0.74		35	49	123	1.17	0.35	0.97	0.42	-0.0130	31.5
8	C	1073		1894		48	18	26	68		1.65	1.24		49	80	130	1.20	0.50	1.64	1.07	0.0075	37.4
8	C	1075		1904		44	11	23	76		1.61	1.10		58	66	118	0.92	0.71	1.50	0.71	-0.0094	35.7
8	C	1076		1898		48	30	27	71		1.54	2.48		57	46	116	1.16	0.49	1.31	-0.05	-0.0162	33.7
8	C	1079		1894		34	37	28	70		0.12	0.00		37	43	133	0.59	0.58	0.73	0.45	-0.0084	39.0
8	I	72			36	19	44	21	70	0.25	0.55	0.00	43	46	32	116	0.59	0.43	0.47	-0.08	-0.0087	
8	I	73				24	37	22	72	0.12	0.16	0.00	55	42	42	115	0.66	0.48	0.27	-0.03	-0.0115	
8	I	75			32	30	41	24	69	0.15	0.74	0.17	43	47	46	64	0.71	0.40	1.01	0.63	0.0102	
8	I	78			36	33	23	26	78	0.65	0.51	0.45	74	46	64	127	1.10	0.42	0.81	0.11	-0.0034	
8	I	79				34	34	21	67	0.65	0.42	0.60	62	44	52	123	1.13	0.42	0.83	1.09	-0.0029	
8	I	1072		1904		18	37	14	70		0.05	0.00		46	43	132	1.10	0.23	0.65	0.59	0.0007	38.7
8	I	1074		1910		26	14	15	66		0.84	0.69		32	58	125	2.20	0.34	1.94	1.79	0.0337	36.6
8	I	1077		1899		20	39	19	70		0.00	0.00		48	33	117	0.57	0.68	0.41	0.38	-0.0047	38.8
8	I	1078		1892		28	28	24	86		0.06	0.12		37	51	120	0.77	0.23	0.56	0.38	-0.0022	36.7
8	I	1080				25	16	22	71		0.04	0.00		53	60	130	1.08	0.43	1.80	-0.19	0.0147	39.4
9	C	81			49	57	39	34	70	1.88	0.70	1.80	65	51	53	91	1.29	0.33	0.77	1.08	-0.0118	
9	C	83				65	23	30	61	5.06	2.58	2.25	93	51	63	110	1.45	0.28	0.92	0.93	-0.0111	
9	C	85				56	25	31	62	5.39	3.30	1.73	66	44	58	121	1.37	0.35	1.31	1.00	-0.0136	
9	C	88				51	28	39	80	2.62	2.02	1.49	64	49	60	128	0.92	0.32	0.77	0.75	-0.0056	
9	C	89				58	37	38	65	2.17	0.96	0.41	62	60	46		0.70	0.46	0.36	0.09	-0.0080	
9	C	1081		1862		47	32	40	78		0.84	0.71		40	67	120	0.96	0.44	0.84	-0.47	-0.0125	36.3
9	C	1083				59	18	34	71		1.43	9.12		42	60	124	0.59	0.32	0.49	0.17	-0.0040	32.2
9	C	1084				50	34	29	58		0.00	0.93		34	64	128	1.34	0.38	0.86	0.75	-0.0079	39.7
9	C	1086				56	25	30	40		2.18	1.24		59	54	117	0.48	0.32	0.32	0.19	-0.0028	34.7
9	C	1087				56	32	47	75		0.63	0.47		57	61	116	0.64	0.68	0.64	0.89	-0.0166	36.5
9	I	82				27	39	17	60	0.00	0.00	0.11	29	43	38	143	0.81	0.71	0.40	0.08	-0.0207	
9	I	84				26	25	13	38	0.08	0.54	1.01	36	48	27	95	0.39	0.60	0.21	0.00	-0.0110	
9	I	86				26	41	24	56	1.23	1.99	2.99	42	52	48	122	0.59	0.58	0.36	0.00	-0.0127	
9	I	87				27	37	23	70	0.00	0.29	0.37	66	48	39	101	0.47	0.53	0.22	0.03	-0.0102	
9	I	90				28	51	30	50	0.00	0.00	0.04	50	50	41	112	0.62	0.51	0.25	0.21	-0.0064	
9	I	1082				43	25	30	71		0.50	0.54		49	55	116						
9	I	1085		1850		39	25	29	62		0.81	0.85		49	68	127	1.10	0.23	0.91	0.11	-0.0002	32.7
9	I	1088		1851		45	16	20	85		2.50	3.73		52	52	123	1.34	0.27	0.92	0.57	-0.0104	32.1
9	I	1089		1904		35	23	31	58		1.39	0.71		53	49	130	1.07	0.42	1.10	0.56	-0.0120	37.3
9	I	1090		1841		46	30	28	81		0.21	0.37		57	45	102	0.25	0.99	0.32	0.17	-0.0091	33.9
10	C	91			39	63	25	26	50	0.53	0.45	0.53	49			103	0.50	0.36	0.34	-0.04	-0.0063	
10	C	92			50	40	32	25	58	1.13	0.43	0.25	65			120	2.06	0.32	1.95	3.73	0.0036	
10	C	95				25	14	19	54	0.08	0.82	0.61	58			130	1.35	0.39	1.70	0.89	0.0153	
10	C	97			50	41	15	25	58	1.03	0.15	0.23	66			102	1.82	0.37	1.03	1.25	-0.0219	
10	C	99			43	58	21	35	55	1.16	0.38	0.35	54			126	0.70	0.36	0.50	0.47	-0.0084	
10	C	1091				71	25	34	55		0.45	0.53		53	58	134	0.79	0.57	1.39	0.43	0.0098	37.5
10	C	1092		1799		50	18	28	45		0.43	0.25		48	45	122	0.59	0.39	0.61	0.46	-0.0048	38.2
10	C	1093				48	34	33	55		0.90	0.79		56	44	120	0.42	0.37	0.45	0.17	-0.0042	36.9

Site	*Crown*	*Tree*	*Char*	*Start*	*GLI*	*DBH*	*BA*	*Ht*	*%LC*	*Res1*	*Res2*	*Res3*	*Phl1*	*Phl2*	*Phl3*	*Fasc*	*Gr62*	*CV.Gr*	*Gr10*	*Drought*	*Slope*	*%Late*
10	C	1095		1821		55	30	35	53		0.82	0.61		53	51	123	1.36	0.22	0.97	0.60	0.0073	35.3
10	C	1100		1910		32	23	27	61		1.74	1.34		50	56	137	0.85	0.44	1.60	0.51	-0.0006	40.2
10	I	93				19	30	19	52	0.00	0.90	0.79	52			136	0.55	0.55	0.81	0.71	0.0077	
10	I	94				36	11	22	60	0.42	0.20	0.11	73			109	1.73	0.26	1.82	0.86	0.0051	
10	I	96				34	18	27	50	0.24	0.24	0.09	44			116	1.26	0.43	0.81	1.41	-0.0115	
10	I	98				52	28	30	58	0.70	0.28	0.12	48			114	0.91	0.40	0.77	1.57	-0.0001	
10	I	100				41	23	34	39	0.43	1.74	1.34	50			127	0.51	0.48	0.35	0.19	-0.0070	
10	I	1094		1907		22	28	18	63		0.20	0.11		51	47	147	0.68	0.30	0.65	-0.33	-0.0042	43.2
10	I	1096		1907		27	30	25	46		0.24	0.09		52	43	116	2.33	0.21	1.67	0.59	0.0119	43.9
10	I	1097		1907		22	25	23	51		0.15	0.23		45	40	128	0.85	0.37	1.11	0.59	0.0102	41.5
10	I	1098		1910		24	30	22	57		0.28	0.12		49	49	110	0.87	0.42	1.32	0.24	0.0111	39.9
10	I	1099		1910		20	14	17	40		0.38	0.35		52	50	119	1.65	0.23	0.89	0.46	0.0089	38.3
11	C	101			47	50	25	45	77	0.72	0.59	1.45	57	48	56	116	0.52	0.34	0.36	0.00	-0.0022	
11	C	102			45	40	28	85	84	0.30	0.32	0.00	56	36	53	106	0.64	0.34	0.61	-0.10	0.0011	
11	C	105			37	61	28	33	72	5.29	2.27	5.72	55	46	55	112	0.57	0.33	0.45	0.17	0.0001	
11	C	106			44	57	25	30	57	1.16	2.05	0.00	55	30	50	103	0.53	0.34	0.50	0.61	0.0026	
11	C	110			43	45	23	71	81	0.61	0.90	5.18	42	56	52	126	0.60	0.37	0.47	0.13	-0.0015	
11	C	1101				63	16	32	79		3.05	3.88		68	57	117						
11	C	1102				52	32	36	59		2.20	2.35		54	57	133	0.63	0.19	0.26	0.21	0.0015	32.8
11	C	1103				59	32	45	82		0.17	0.76		46	53	118	0.40	0.26	0.35	-0.05	-0.0018	31.9
11	C	1106				62	23	36	70		0.50	0.68		47	67	122	0.80	0.37	0.87	1.21	-0.0022	40.6
11	C	1107		1797		53	32	26	46		1.10	1.40		46	60	127	0.83	0.30	0.76	-0.05	0.0027	31.5
11	I	103			26	35	34	36	69	0.15	0.14	0.13	38	37	41	120	0.59	0.39	0.41	0.35	0.0014	
11	I	104				38	23	21	37	0.28	0.24	0.14	36	39	33	110	0.33	0.42	0.21	0.02	-0.0034	
11	I	107			39	39	39	24	61	0.00	0.00	0.00	44	38	30	107	0.38	0.42	0.25	-0.07	-0.0032	
11	I	108				42	28	32	62	0.45	0.68	1.16	45	70	45	112	0.54	0.41	0.42	0.39	0.0023	
11	I	109			45	38	41	32	70	0.07	0.46	0.27	46	59	41	110	0.50	0.36	0.42	-0.13	-0.0011	
11	I	1104		1803		43	25	37	68		3.46	1.44		53	47	120	0.30	0.46	0.34	-0.09	0.0015	29.7
11	I	1105		1841		39	25	26	75		1.77	0.75		55	48	127	0.46	1.27	1.09	0.55	-0.0169	37.3
11	I	1108		1909		34	21	26	84		0.39	0.14		47	56	132	1.40	0.53	1.44	1.70	-0.0083	30.2
11	I	1109		1922		31	16	24	73		0.93	0.57		49	48	123	1.31	0.36	1.30	1.72	-0.0081	27.5
11	I	1110		1920		38	18	25	57		0.66	0.34		43	75	138	1.25	0.54	1.79	1.85	-0.0020	37.9
12	C	111			44	46	28	46	69	1.43	2.22	3.25	70	50	71	103	1.10	0.31	0.81	0.57	-0.0080	
12	C	114			38	54	30	39	69	1.79	1.01	1.86	63	50	50	119	1.21	0.31	0.79	0.43	-0.0103	
12	C	116			39	45	48	102	79	1.70	1.57	3.51	45	54	47	123	0.63	0.31	0.61	0.04	0.0012	
12	C	118				40	51	32	61	1.64	0.39	5.23	72	35	74	110	0.96	0.37	1.13	1.08	0.0106	
12	C	119			36	48	28	34	60	0.65	0.57	0.88	69	57	50	111						
12	C	1112		1831		46	41	43	70		1.25	2.23		60	52	109	1.40	0.29	1.28	-0.13	0.0130	31.6
12	C	1113				55	32	31	52		0.66	0.82		50	65	145	0.89	0.46	0.65	0.46	0.0026	39.8
12	C	1115		1848		49	21	51	72		0.34	0.35		49	61	130	0.51	0.45	0.33	0.22	-0.0058	35.4
12	C	1116				62	23	25	50		0.13	0.29		53	62	138	1.18	0.66	1.61	0.21	0.0197	33.7
12	C	1117				56	32	32	54		0.57	0.86		67	44	138	1.02	0.28	1.08	0.34	0.0022	33.6
12	I	112				37	51	29	45	2.33	1.53	0.84	55	54	37	114	0.43	0.31	0.51	0.43	0.0025	
12	I	113				30	28	22	48	0.31	0.22	1.04	60	63	46	119	0.71	0.47	0.52	0.04	-0.0096	
12	I	115				39	44	34	67	1.02	0.46	0.63	52	45	44	116	1.09	0.35	0.83	0.52	-0.0058	
12	I	117				31	32	22	53	5.20	2.21	2.93	43	39	37	124	0.48	0.54	0.31	-0.02	-0.0059	
12	I	120				49	30	36	72	2.11	0.95	1.11	59	48	39	125						

Site	*Crown*	*Tree*	*Char*	*Start*	*GLI*	*DBH*	*BA*	*Ht*	*%LC*	*Res1*	*Res2*	*Res3*	*Phl1*	*Phl2*	*Phl3*	*Fasc*	*Gr62*	*CV.Gr*	*Gr10*	*Drought*	*Slope*	*%Late*
12	I	1111		1843		36	39	30	69		0.97	0.86		44	49	134	1.36	0.28	1.45	-0.25	0.0126	40.2
12	I	1114				32	39	34	64		1.05	0.70		37	53	129	0.76	0.32	0.91	0.39	0.0068	41.9
12	I	1118		1885		36	37	40	76		1.24	2.36		52	62	127	0.63	0.54	0.81	0.26	-0.0083	42.2
12	I	1119				40	18	27	77		0.67	0.61		68	58	139	1.17	0.35	1.08	0.09	0.0174	34.8
12	I	1120		1868		40	25	22	52		0.44			43	62	120	1.34	0.68	1.85	1.63	0.0004	43.7

Site = Site ID (see Fig. 2.3). *Crown* = crown class (codominant or intermediate). *Tree* = Tree ID.
Char = height of trunk charring from prescribed burn in April 1998 (m). *Start* = year of germination (age at 1.5 m + 5 years)
GLI = gap light index (% light transmission through canopy). *DBH* = diameter at breast height (cm). *BA* = basal area (m2 / ha).
Ht = tree height (m). *%LC* = percent live crown (% of total height).
Res1, Res2, Res3 = resin flow / wound in Aug 1997, July 1998, and Aug 1998, respectively (g / 1.23 cm2)
Phl1, Phl2, Phl3 = phloem thickness in Aug 1997, July 1998, and Aug 1998, respectively (mg dry mass / 1.23 cm2)
Fasc = fascicle length (mm). G*r62* = average radial growth for 62 years from 1935 to 1996 (mm / year).
Gr10 = average radial growth for 10 years from 1987 to 1996 (mm / year)
CVGrow = coefficient of interannual variation in annual radial growth (SD / mean).
Drought = reduction in annual radial growth due to drought: mm growth in 1986 (predrought) - mm growth in 1990 (drought).
Slope = slope from linear regression of annual radial growth vs year from 1935 to 1996.
Latewood = percent of radial growth comprised of latewood tracheids vs earlywood tracheids.

Neutron probe measurements in September 1998 (see Chapter 2).

	6" depth				12" depth				18" depth				24" depth				30 " depth			
	Plot 1		Plot 2		Plot 1		Plot 2		Plot 1		Plot 2		Plot 1		Plot 2		Plot 1		Plot 2	
Site	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
1	1262	1253	1183	1195	1329	1336	1161	1173	1263	1257	1196	1195	1313	1284	1437	1431				
2	1672	1663	1437	1466	1935	1844	1977	1973	2003	1984	2202	2240								
3	926	971	1129	1125	1154	1148	1242	1245	1136	1106	1409	1360	1219	1196	1575	1493	1388	1390		
4	1429	1455	1680	1714	1771	1780	1959	1940	2437	2479	2169	2143								
5	1358	1427	1184	1171	1539	1527	1222	1209	1939	1940	1304	1260								
6	1593	1637	1035	1071	1977	1997	1095	1069			1133	1146								
7	1672	1763	1676	1617	1880	1910	1914	1871	2006	2070	2101	2077								
8	1566	1545	1527	1534	1963	1954	1861	1877	2262	2282	1986	1962								
9	1820	1892	1363	1376	2203	2159	1312	1333	2861	2876	1578	1581			2228	2198				
10	2076	2199			2459	2451			3113	3044										
11	1333	1398	1538	1600	1734	1715	1746	1743	1806	1763										
12	1418	1484	1074	1061	1667	1664	1364	1410	2343	2319	1760	1735			2574	2535				

	Plot 1				
Site	6"	12"	18"	24"	30"
1	1258	1333	1260	1299	
2	1668	1890	1994		
3	949	1151	1121	1208	1389
4	1442	1776	2458		
5	1393	1533	1940		
6	1615	1987			
7	1718	1895	2038		
8	1556	1959	2272		
9	1856	2181	2869		
10	2138	2455	3079		
11	1366	1725	1785		
12	1451	1666	2331		

	Plot 2				
	6"	12"	18"	24"	30"
	1189	1167	1196	1434	
	1452	1975	2221		
	1127	1244	1385	1534	
	1697	1950	2156		
	1178	1216	1282		
	1053	1082	1140		
	1647	1893	2089		
	1531	1869	1974		
	1370	1323	1580	2213	
	1569	1745			
	1068	1387	1748	2555	

	Averaged across plots within a site				
	6"	12"	18"	24"	30"
	1223	1250	1228	1366	
	1560	1932	2107		
	1038	1197	1253	1371	
	1570	1863	2307		
	1285	1374	1611		
	1334	1535			
	1682	1894	2064		
	1543	1914	2123		
	1613	1752	2224		
	2138	2455	3079		
	1467	1735	1785		
	1259	1526	2039		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/16/97	401	Undisturbed	*P. resin.*	Fire	Ipsenol		1				
7/16/97	401	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/16/97	401	Undisturbed	*P. resin.*	Fire	Both	5		1			
7/16/97	402	Undisturbed	*P. resin.*	Fire	Ipsenol		4		1		
7/16/97	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	3			3		
7/16/97	402	Undisturbed	*P. resin.*	Fire	Both	4		1	20		
7/16/97	403	Undisturbed	*P. resin.*	Fire	Ipsenol		4		6		
7/16/97	403	Undisturbed	*P. resin.*	Fire	Ipsdienol				3		
7/16/97	403	Undisturbed	*P. resin.*	Fire	Both	6	1		2		
7/16/97	404	Undisturbed	*P. resin.*	NoFire	Ipsenol		2		1		
7/16/97	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	24		1	1		
7/16/97	404	Undisturbed	*P. resin.*	NoFire	Both	18					
7/16/97	405	Undisturbed	*P. resin.*	NoFire	Ipsenol						
7/16/97	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	163		6	13		
7/16/97	405	Undisturbed	*P. resin.*	NoFire	Both	63	2	1	2		
7/16/97	406	Undisturbed	*P. resin.*	Fire	Ipsenol	1					2
7/16/97	406	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/16/97	406	Undisturbed	*P. resin.*	Fire	Both	1					
7/16/97	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/16/97	407	Undisturbed	*P. resin.*	Fire	Ipsdienol	2			1		
7/16/97	407	Undisturbed	*P. resin.*	Fire	Both	5			1		
7/16/97	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/16/97	408	Undisturbed	*P. resin.*	Fire	Ipsdienol	38		4	2		
7/16/97	408	Undisturbed	*P. resin.*	Fire	Both	5		2			
7/16/97	409	Undisturbed	*P. resin.*	NoFire	Ipsenol	3					
7/16/97	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	25				1	
7/16/97	409	Undisturbed	*P. resin.*	NoFire	Both	1					
7/16/97	410	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/16/97	410	Disturbed	*P. resin.*	NoFire	Ipsdienol	31					
7/16/97	410	Disturbed	*P. resin.*	NoFire	Both	7	2				
7/16/97	411	NearDisturb	*P. resin.*	Fire	Ipsenol				1		
7/16/97	411	NearDisturb	*P. resin.*	Fire	Ipsdienol	18					
7/16/97	411	NearDisturb	*P. resin.*	Fire	Both	10					
7/16/97	412	Disturbed	*P. resin.*	Fire	Ipsenol						
7/16/97	412	Disturbed	*P. resin.*	Fire	Ipsdienol			1			
7/16/97	412	Disturbed	*P. resin.*	Fire	Both	1					
7/16/97	413	NearDisturb	*P. resin.*	Fire	Ipsenol						
7/16/97	413	NearDisturb	*P. resin.*	Fire	Ipsdienol	111		5			
7/16/97	413	NearDisturb	*P. resin.*	Fire	Both	157		4			
7/16/97	414	Disturbed	*P. resin.*	Fire	Ipsenol						
7/16/97	414	Disturbed	*P. resin.*	Fire	Ipsdienol						
7/16/97	414	Disturbed	*P. resin.*	Fire	Both						
7/16/97	415	NearDisturb	*P. resin.*	NoFire	Ipsenol	5	1		1		
7/16/97	415	NearDisturb	*P. resin.*	NoFire	Ipsdienol	109		4			
7/16/97	415	NearDisturb	*P. resin.*	NoFire	Both	43		3			
7/16/97	416	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/16/97	416	Disturbed	*P. resin.*	NoFire	Ipsdienol	48		2			
7/16/97	416	Disturbed	*P. resin.*	NoFire	Both	96		7	1		
7/16/97	417	NearDisturb	*P. resin.*	NoFire	Ipsenol	11	32				
7/16/97	417	NearDisturb	*P. resin.*	NoFire	Ipsdienol	12			2	2	
7/16/97	417	NearDisturb	*P. resin.*	NoFire	Both	3	1				
7/16/97	418	Disturbed	*P. resin.*	NoFire	Ipsenol	1					

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/16/97	418	Disturbed	*P. resin.*	NoFire	Ipsdienol	43		2			
7/16/97	418	Disturbed	*P. resin.*	NoFire	Both	41		5	1		
7/16/97	419	NearDisturb	*P. resin.*	NoFire	Ipsenol						
7/16/97	419	NearDisturb	*P. resin.*	NoFire	Ipsdienol	458		20			
7/16/97	419	NearDisturb	*P. resin.*	NoFire	Both	241		5	1		
7/16/97	420	Undisturbed	Mixed	NoFire	Ipsenol		1				
7/16/97	420	Undisturbed	Mixed	NoFire	Ipsdienol						
7/16/97	420	Undisturbed	Mixed	NoFire	Both	2		3			
7/16/97	421	Undisturbed	*P strobus*	NoFire	Ipsenol		9		1		
7/16/97	421	Undisturbed	*P strobus*	NoFire	Ipsdienol	40		4			
7/16/97	421	Undisturbed	*P strobus*	NoFire	Both	3	1		1		
7/16/97	422	NearDisturb	*P banks*	NoFire	Ipsenol		4				
7/16/97	422	NearDisturb	*P banks*	NoFire	Ipsdienol	67		1			
7/16/97	422	NearDisturb	*P banks*	NoFire	Both	2			2		
7/16/97	424	plantation	*P. resin.*	NoFire	Ipsenol				1	1	
7/16/97	424	plantation	*P. resin.*	NoFire	Ipsdienol	7		1	1		1
7/16/97	424	plantation	*P. resin.*	NoFire	Both	6		5	1	1	
7/16/97	425	plantation	*P. resin.*	NoFire	Ipsenol		2		1		
7/16/97	425	plantation	*P. resin.*	NoFire	Ipsdienol	1					
7/16/97	425	plantation	*P. resin.*	NoFire	Both	3			1		
7/16/97	426	plantation	*P. resin.*	NoFire	Ipsenol	2	1		3		
7/16/97	426	plantation	*P. resin.*	NoFire	Ipsdienol	107		8	3		
7/16/97	426	plantation	*P. resin.*	NoFire	Both	274	3	19	39	1	
7/16/97	427	plantation	*P. resin.*	NoFire	Ipsenol	2	2		2		
7/16/97	427	plantation	*P. resin.*	NoFire	Ipsdienol	28		4	8		
7/16/97	427	plantation	*P. resin.*	NoFire	Both	41		54	15		
7/28/97	401	Undisturbed	*P. resin.*	NoFire	Ipsenol		1				
7/28/97	401	Undisturbed	*P. resin.*	NoFire	Ipsdienol	3			1		
7/28/97	401	Undisturbed	*P. resin.*	NoFire	Both	20		11			
7/28/97	402	Undisturbed	*P. resin.*	NoFire	Ipsenol		7		3		
7/28/97	402	Undisturbed	*P. resin.*	NoFire	Ipsdienol	10			12	1	
7/28/97	402	Undisturbed	*P. resin.*	NoFire	Both	9		9	8		
7/28/97	403	Undisturbed	*P. resin.*	NoFire	Ipsenol	1	2		2		
7/28/97	403	Undisturbed	*P. resin.*	NoFire	Ipsdienol	42			2	1	
7/28/97	403	Undisturbed	*P. resin.*	NoFire	Both	8		8	4	2	
7/28/97	404	Undisturbed	*P. resin.*	NoFire	Ipsenol	1	1				
7/28/97	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	9					
7/28/97	404	Undisturbed	*P. resin.*	NoFire	Both	74		3	1		
7/28/97	405	Undisturbed	*P. resin.*	NoFire	Ipsenol	3	1				
7/28/97	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	87			3		
7/28/97	405	Undisturbed	*P. resin.*	NoFire	Both	60		10	2		
7/28/97	406	Undisturbed	*P. resin.*	NoFire	Ipsenol	1	2				
7/28/97	406	Undisturbed	*P. resin.*	NoFire	Ipsdienol	7					
7/28/97	406	Undisturbed	*P. resin.*	NoFire	Both						
7/28/97	407	Undisturbed	*P. resin.*	NoFire	Ipsenol				1		
7/28/97	407	Undisturbed	*P. resin.*	NoFire	Ipsdienol	6			1		
7/28/97	407	Undisturbed	*P. resin.*	NoFire	Both	2					
7/28/97	408	Undisturbed	*P. resin.*	NoFire	Ipsenol	2	1				
7/28/97	408	Undisturbed	*P. resin.*	NoFire	Ipsdienol	77		2	1		
7/28/97	408	Undisturbed	*P. resin.*	NoFire	Both	8					
7/28/97	409	Undisturbed	*P. resin.*	NoFire	Ipsenol		2				
7/28/97	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol						

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/28/97	409	Undisturbed	*P. resin.*	NoFire	Both						
7/28/97	410	Undisturbed	Mixed	NoFire	Ipsenol						
7/28/97	410	Undisturbed	Mixed	NoFire	Ipsdienol	9					
7/28/97	410	Undisturbed	Mixed	NoFire	Both	39					
7/28/97	411	Disturbed	*P. resin.*	NoFire	Ipsenol	11	1		3		
7/28/97	411	Disturbed	*P. resin.*	NoFire	Ipsdienol	73			1		
7/28/97	411	Disturbed	*P. resin.*	NoFire	Both	194		4	1		
7/28/97	412	NearDisturb	*P. resin.*	NoFire	Ipsenol				1		
7/28/97	412	NearDisturb	*P. resin.*	NoFire	Ipsdienol	13		1			
7/28/97	412	NearDisturb	*P. resin.*	NoFire	Both	15		1			
7/28/97	413	Disturbed	*P. resin.*	NoFire	Ipsenol	2	1				
7/28/97	413	Disturbed	*P. resin.*	NoFire	Ipsdienol	271					
7/28/97	413	Disturbed	*P. resin.*	NoFire	Both	522			1		
7/28/97	414	NearDisturb	*P. resin.*	NoFire	Ipsenol	1					
7/28/97	414	NearDisturb	*P. resin.*	NoFire	Ipsdienol	18					
7/28/97	414	NearDisturb	*P. resin.*	NoFire	Both	15					
7/28/97	415	Disturbed	*P. resin.*	NoFire	Ipsenol	5	5				
7/28/97	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	218			1		
7/28/97	415	Disturbed	*P. resin.*	NoFire	Both	123		3	6		
7/28/97	416	NearDisturb	*P. resin.*	NoFire	Ipsenol	5	4				
7/28/97	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	117		3			
7/28/97	416	NearDisturb	*P. resin.*	NoFire	Both	135		1			
7/28/97	417	Disturbed	*P. resin.*	NoFire	Ipsenol	3	3		1		
7/28/97	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	31					
7/28/97	417	Disturbed	*P. resin.*	NoFire	Both	64			2		
7/28/97	418	NearDisturb	*P. resin.*	NoFire	Ipsenol		2				1
7/28/97	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	58					
7/28/97	418	NearDisturb	*P. resin.*	NoFire	Both	73		5			
7/28/97	419	Disturbed	*P. resin.*	NoFire	Ipsenol		3		1		
7/28/97	419	Disturbed	*P. resin.*	NoFire	Ipsdienol	22					
7/28/97	419	Disturbed	*P. resin.*	NoFire	Both	524					
7/28/97	420	NearDisturb	*P. resin.*	NoFire	Ipsenol	1	1				
7/28/97	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	23		1			
7/28/97	420	NearDisturb	*P. resin.*	NoFire	Both	73		2		1	
7/28/97	421	Undisturbed	Mixed	NoFire	Ipsenol	2	1				
7/28/97	421	Undisturbed	Mixed	NoFire	Ipsdienol	37		1			
7/28/97	421	Undisturbed	Mixed	NoFire	Both	2	1				
7/28/97	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
7/28/97	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	29					
7/28/97	422	Undisturbed	*P strobus*	NoFire	Both	5	2		1		
7/28/97	423	NearDisturb	*P banks*	NoFire	Ipsenol	7	3		7		
7/28/97	423	NearDisturb	*P banks*	NoFire	Ipsdienol	173			13		1
7/28/97	423	NearDisturb	*P banks*	NoFire	Both	456		75	8		
7/28/97	424	plantation	*P. resin.*	NoFire	Ipsenol		2		3		
7/28/97	424	plantation	*P. resin.*	NoFire	Ipsdienol	6			8		
7/28/97	424	plantation	*P. resin.*	NoFire	Both	14		10	3		
7/28/97	425	plantation	*P. resin.*	NoFire	Ipsenol						
7/28/97	425	plantation	*P. resin.*	NoFire	Ipsdienol				1		
7/28/97	425	plantation	*P. resin.*	NoFire	Both	27					
7/28/97	426	plantation	*P. resin.*	NoFire	Ipsenol						
7/28/97	426	plantation	*P. resin.*	NoFire	Ipsdienol						
7/28/97	426	plantation	*P. resin.*	NoFire	Both						

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/28/97	427	plantation	*P. resin.*	NoFire	Ipsenol						
7/28/97	427	plantation	*P. resin.*	NoFire	Ipsdienol	6			1		
7/28/97	427	plantation	*P. resin.*	NoFire	Both						
8/18/97	401	Undisturbed	*P. resin.*	NoFire	Ipsenol		2				
8/18/97	401	Undisturbed	*P. resin.*	NoFire	Ipsdienol	41					
8/18/97	401	Undisturbed	*P. resin.*	NoFire	Both			1			
8/18/97	402	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		1		
8/18/97	402	Undisturbed	*P. resin.*	NoFire	Ipsdienol	11			2		
8/18/97	402	Undisturbed	*P. resin.*	NoFire	Both	11		6	7		
8/18/97	403	Undisturbed	*P. resin.*	NoFire	Ipsenol	2	1		1	3	
8/18/97	403	Undisturbed	*P. resin.*	NoFire	Ipsdienol	33					
8/18/97	403	Undisturbed	*P. resin.*	NoFire	Both	2			6		
8/18/97	404	Undisturbed	*P. resin.*	NoFire	Ipsenol	2					
8/18/97	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	14					
8/18/97	404	Undisturbed	*P. resin.*	NoFire	Both	3					
8/18/97	405	Undisturbed	*P. resin.*	NoFire	Ipsenol	1	3				
8/18/97	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	44		2	1		
8/18/97	405	Undisturbed	*P. resin.*	NoFire	Both	8					
8/18/97	406	Undisturbed	*P. resin.*	NoFire	Ipsenol	1	1				
8/18/97	406	Undisturbed	*P. resin.*	NoFire	Ipsdienol	6					
8/18/97	406	Undisturbed	*P. resin.*	NoFire	Both	2					
8/18/97	407	Undisturbed	*P. resin.*	NoFire	Ipsenol	2	3				
8/18/97	407	Undisturbed	*P. resin.*	NoFire	Ipsdienol	2					
8/18/97	407	Undisturbed	*P. resin.*	NoFire	Both				1		
8/18/97	408	Undisturbed	*P. resin.*	NoFire	Ipsenol		4		1		
8/18/97	408	Undisturbed	*P. resin.*	NoFire	Ipsdienol						
8/18/97	408	Undisturbed	*P. resin.*	NoFire	Both	12		4			
8/18/97	409	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		1		
8/18/97	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	1					
8/18/97	409	Undisturbed	*P. resin.*	NoFire	Both			1			
8/18/97	410	Undisturbed	Mixed	NoFire	Ipsenol						
8/18/97	410	Undisturbed	Mixed	NoFire	Ipsdienol	9					
8/18/97	410	Undisturbed	Mixed	NoFire	Both	39					
8/18/97	411	Disturbed	*P. resin.*	NoFire	Ipsenol	2	4		1		
8/18/97	411	Disturbed	*P. resin.*	NoFire	Ipsdienol	118			1		
8/18/97	411	Disturbed	*P. resin.*	NoFire	Both	3		1			
8/18/97	412	NearDisturb	*P. resin.*	NoFire	Ipsenol						
8/18/97	412	NearDisturb	*P. resin.*	NoFire	Ipsdienol	83					
8/18/97	412	NearDisturb	*P. resin.*	NoFire	Both	2					
8/18/97	413	Disturbed	*P. resin.*	NoFire	Ipsenol	6	3				
8/18/97	413	Disturbed	*P. resin.*	NoFire	Ipsdienol	221					
8/18/97	413	Disturbed	*P. resin.*	NoFire	Both	15		1			
8/18/97	414	NearDisturb	*P. resin.*	NoFire	Ipsenol						
8/18/97	414	NearDisturb	*P. resin.*	NoFire	Ipsdienol	47					
8/18/97	414	NearDisturb	*P. resin.*	NoFire	Both	5					
8/18/97	415	Disturbed	*P. resin.*	NoFire	Ipsenol	5	10		1		
8/18/97	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	114					
8/18/97	415	Disturbed	*P. resin.*	NoFire	Both	29			2		
8/18/97	416	NearDisturb	*P. resin.*	NoFire	Ipsenol	1	5				
8/18/97	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	78					
8/18/97	416	NearDisturb	*P. resin.*	NoFire	Both			1	1		
8/18/97	417	Disturbed	*P. resin.*	NoFire	Ipsenol	1	4		1		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
8/18/97	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	17					
8/18/97	417	Disturbed	*P. resin.*	NoFire	Both	25			4		
8/18/97	418	NearDisturb	*P. resin.*	NoFire	Ipsenol				1		
8/18/97	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	30			2		
8/18/97	418	NearDisturb	*P. resin.*	NoFire	Both	11		1	3		
8/18/97	419	Disturbed	*P. resin.*	NoFire	Ipsenol	6	3				
8/18/97	419	Disturbed	*P. resin.*	NoFire	Ipsdienol	322					
8/18/97	419	Disturbed	*P. resin.*	NoFire	Both	11					
8/18/97	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
8/18/97	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	11					
8/18/97	420	NearDisturb	*P. resin.*	NoFire	Both						
8/18/97	421	Undisturbed	Mixed	NoFire	Ipsenol	1	1				
8/18/97	421	Undisturbed	Mixed	NoFire	Ipsdienol	3					
8/18/97	421	Undisturbed	Mixed	NoFire	Both	7					
8/18/97	422	Undisturbed	*P strobus*	NoFire	Ipsenol		2				
8/18/97	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	99					
8/18/97	422	Undisturbed	*P strobus*	NoFire	Both	2					
8/18/97	423	NearDisturb	*P banks*	NoFire	Ipsenol						
8/18/97	423	NearDisturb	*P banks*	NoFire	Ipsdienol	40					
8/18/97	423	NearDisturb	*P banks*	NoFire	Both	3					
8/18/97	424	plantation	*P. resin.*	NoFire	Ipsenol	6	4		5		
8/18/97	424	plantation	*P. resin.*	NoFire	Ipsdienol	8			1		
8/18/97	424	plantation	*P. resin.*	NoFire	Both	3			5		
8/18/97	425	plantation	*P. resin.*	NoFire	Ipsenol		2				
8/18/97	425	plantation	*P. resin.*	NoFire	Ipsdienol						
8/18/97	425	plantation	*P. resin.*	NoFire	Both						
8/18/97	426	plantation	*P. resin.*	NoFire	Ipsenol	8		2	5		
8/18/97	426	plantation	*P. resin.*	NoFire	Ipsdienol	31		8	1		
8/18/97	426	plantation	*P. resin.*	NoFire	Both	10		6	8		
8/18/97	427	plantation	*P. resin.*	NoFire	Ipsenol	6		2			
8/18/97	427	plantation	*P. resin.*	NoFire	Ipsdienol	4		1	2		
8/18/97	427	plantation	*P. resin.*	NoFire	Both	3		6	3	1	
9/10/97	401	Undisturbed	*P. resin.*	NoFire	Ipsenol		1				
9/10/97	401	Undisturbed	*P. resin.*	NoFire	Ipsdienol	85					
9/10/97	401	Undisturbed	*P. resin.*	NoFire	Both	11	1		1		
9/10/97	402	Undisturbed	*P. resin.*	NoFire	Ipsenol	2	13				
9/10/97	402	Undisturbed	*P. resin.*	NoFire	Ipsdienol	96					
9/10/97	402	Undisturbed	*P. resin.*	NoFire	Both	18		10	1		
9/10/97	403	Undisturbed	*P. resin.*	NoFire	Ipsenol	1	5				
9/10/97	403	Undisturbed	*P. resin.*	NoFire	Ipsdienol	106			1		
9/10/97	403	Undisturbed	*P. resin.*	NoFire	Both	13		1	1		
9/10/97	404	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/10/97	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	49					
9/10/97	404	Undisturbed	*P. resin.*	NoFire	Both			1			
9/10/97	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		11	1	3		
9/10/97	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	142					
9/10/97	405	Undisturbed	*P. resin.*	NoFire	Both			4			
9/10/97	406	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/10/97	406	Undisturbed	*P. resin.*	NoFire	Ipsdienol	28					
9/10/97	406	Undisturbed	*P. resin.*	NoFire	Both	6			1		
9/10/97	407	Undisturbed	*P. resin.*	NoFire	Ipsenol		1				
9/10/97	407	Undisturbed	*P. resin.*	NoFire	Ipsdienol	88					

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
9/10/97	407	Undisturbed	*P. resin.*	NoFire	Both	17		3			
9/10/97	408	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/10/97	408	Undisturbed	*P. resin.*	NoFire	Ipsdienol	39					
9/10/97	408	Undisturbed	*P. resin.*	NoFire	Both	1					
9/10/97	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/10/97	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	7					
9/10/97	409	Undisturbed	*P. resin.*	NoFire	Both	4	1				
9/10/97	410	Undisturbed	Mixed	NoFire	Ipsenol						
9/10/97	410	Undisturbed	Mixed	NoFire	Ipsdienol	244					
9/10/97	410	Undisturbed	Mixed	NoFire	Both	3					
9/10/97	411	Disturbed	*P. resin.*	NoFire	Ipsenol	3			1		
9/10/97	411	Disturbed	*P. resin.*	NoFire	Ipsdienol	252		1	5		
9/10/97	411	Disturbed	*P. resin.*	NoFire	Both	11			1		
9/10/97	412	NearDisturb	*P. resin.*	NoFire	Ipsenol	2					
9/10/97	412	NearDisturb	*P. resin.*	NoFire	Ipsdienol	23					
9/10/97	412	NearDisturb	*P. resin.*	NoFire	Both						
9/10/97	413	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/10/97	413	Disturbed	*P. resin.*	NoFire	Ipsdienol	161					
9/10/97	413	Disturbed	*P. resin.*	NoFire	Both	30		1			
9/10/97	414	NearDisturb	*P. resin.*	NoFire	Ipsenol						
9/10/97	414	NearDisturb	*P. resin.*	NoFire	Ipsdienol	37					
9/10/97	414	NearDisturb	*P. resin.*	NoFire	Both	13					
9/10/97	415	Disturbed	*P. resin.*	NoFire	Ipsenol	3					
9/10/97	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	201					
9/10/97	415	Disturbed	*P. resin.*	NoFire	Both	28					
9/10/97	416	NearDisturb	*P. resin.*	NoFire	Ipsenol	3	4				
9/10/97	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	165					
9/10/97	416	NearDisturb	*P. resin.*	NoFire	Both	9	1	1	1		
9/10/97	417	Disturbed	*P. resin.*	NoFire	Ipsenol		2				
9/10/97	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	65	1			1	
9/10/97	417	Disturbed	*P. resin.*	NoFire	Both	16			1		
9/10/97	418	NearDisturb	*P. resin.*	NoFire	Ipsenol	1	6				
9/10/97	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	41			2		
9/10/97	418	NearDisturb	*P. resin.*	NoFire	Both	1			1		
9/10/97	419	Disturbed	*P. resin.*	NoFire	Ipsenol	2					
9/10/97	419	Disturbed	*P. resin.*	NoFire	Ipsdienol	596					
9/10/97	419	Disturbed	*P. resin.*	NoFire	Both	242			1	1	
9/10/97	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
9/10/97	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	141			1		
9/10/97	420	NearDisturb	*P. resin.*	NoFire	Both	8					
9/10/97	421	Undisturbed	Mixed	NoFire	Ipsenol	1	2				
9/10/97	421	Undisturbed	Mixed	NoFire	Ipsdienol	236					
9/10/97	421	Undisturbed	Mixed	NoFire	Both	6					
9/10/97	422	Undisturbed	*P strobus*	NoFire	Ipsenol	1	1				
9/10/97	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	109					
9/10/97	422	Undisturbed	*P strobus*	NoFire	Both	30					
9/10/97	423	NearDisturb	*P banks*	NoFire	Ipsenol		2				
9/10/97	423	NearDisturb	*P banks*	NoFire	Ipsdienol	177			3		
9/10/97	423	NearDisturb	*P banks*	NoFire	Both	6					
9/10/97	424	plantation	*P. resin.*	NoFire	Ipsenol	1	14		7		
9/10/97	424	plantation	*P. resin.*	NoFire	Ipsdienol	124					
9/10/97	424	plantation	*P. resin.*	NoFire	Both	4			4		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
9/10/97	425	plantation	*P. resin.*	NoFire	Ipsenol	6					
9/10/97	425	plantation	*P. resin.*	NoFire	Ipsdienol	65			36		
9/10/97	425	plantation	*P. resin.*	NoFire	Both	23					
9/10/97	426	plantation	*P. resin.*	NoFire	Ipsenol	1	17				
9/10/97	426	plantation	*P. resin.*	NoFire	Ipsdienol	41					
9/10/97	426	plantation	*P. resin.*	NoFire	Both	36		2	6	1	
9/10/97	427	plantation	*P. resin.*	NoFire	Ipsenol						
9/10/97	427	plantation	*P. resin.*	NoFire	Ipsdienol	26					
9/10/97	427	plantation	*P. resin.*	NoFire	Both	10		6	6		
5/13/98	401	Undisturbed	*P. resin.*	Fire	both			1	2		
5/13/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol	2			1		
5/13/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol	1	2		5		
5/13/98	402	Undisturbed	*P. resin.*	Fire	both			12	15		
5/13/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	4			1		
5/13/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol		17		7		
5/13/98	403	Undisturbed	*P. resin.*	Fire	both				3		
5/13/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol						
5/13/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol		2		2		
5/13/98	404	Undisturbed	*P. resin.*	NoFire	both	2		2	6		
5/13/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	9			2		
5/13/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		7		
5/13/98	405	Undisturbed	*P. resin.*	NoFire	both	1			3		
5/13/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	1			4		
5/13/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		2		1		
5/13/98	406	Undisturbed	*P. resin.*	Fire	both	3	1		1		
5/13/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol		14				
5/13/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol		51		12		
5/13/98	407	Undisturbed	*P. resin.*	Fire	both	2			3		
5/13/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol				1		
5/13/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol		2		1		
5/13/98	408	Undisturbed	*P. resin.*	Fire	both		3	1	28		
5/13/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol	7			6		
5/13/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol		1		9		
5/13/98	409	Undisturbed	*P. resin.*	NoFire	both	1			1		
5/13/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	2					
5/13/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol		2				
5/13/98	411	Disturbed	*P. resin.*	Fire	both						
5/13/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol	3			13		
5/13/98	411	Disturbed	*P. resin.*	Fire	Ipsenol		5		21		
5/13/98	412	NearDisturb	*P. resin.*	Fire	both	1			5		2
5/13/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol	21			2	1	
5/13/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol		55		85		
5/13/98	413	Disturbed	*P. resin.*	Fire	both				43	1	
5/13/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol	23					
5/13/98	413	Disturbed	*P. resin.*	Fire	Ipsenol		45		6		
5/13/98	414	NearDisturb	*P. resin.*	Fire	both						
5/13/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol	4					
5/13/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol		6		1		
5/13/98	415	Disturbed	*P. resin.*	NoFire	both	6			1		
5/13/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol						
5/13/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol		41		3		
5/13/98	416	NearDisturb	*P. resin.*	NoFire	both						

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
5/13/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	1			1		
5/13/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol		1				
5/13/98	417	Disturbed	*P. resin.*	NoFire	both	3	7		1	2	1
5/13/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	8					
5/13/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol	1	86		6	1	
5/13/98	418	NearDisturb	*P. resin.*	NoFire	both	1	2		9		2
5/13/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	2			2		
5/13/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol		82	1	8		
5/13/98	419	Disturbed	*P. resin.*	NoFire	both				1	1	
5/13/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol						
5/13/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol		5				
5/13/98	420	NearDisturb	*P. resin.*	NoFire	both			4	3		
5/13/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	3			3		
5/13/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol		32		6		
5/13/98	421	Undisturbed	Mixed	NoFire	both			1			
5/13/98	421	Undisturbed	Mixed	NoFire	Ipsdienol						
5/13/98	421	Undisturbed	Mixed	NoFire	Ipsenol						
5/13/98	422	Undisturbed	*P strobus*	NoFire	both	1	1				
5/13/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol			1			
5/13/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
5/13/98	423	NearDisturb	*P banks*	NoFire	both			5	6		
5/13/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	2			5		
5/13/98	423	NearDisturb	*P banks*	NoFire	Ipsenol	3	19		3		
5/13/98	424	plantation	*P. resin.*	NoFire	both			1	7		
5/13/98	424	plantation	*P. resin.*	NoFire	Ipsdienol				15		
5/13/98	424	plantation	*P. resin.*	NoFire	Ipsenol		3		8		
5/13/98	425	plantation	*P. resin.*	NoFire	both			1			
5/13/98	425	plantation	*P. resin.*	NoFire	Ipsdienol						
5/13/98	425	plantation	*P. resin.*	NoFire	Ipsenol						
5/13/98	426	plantation	*P. resin.*	NoFire	both				1		
5/13/98	426	plantation	*P. resin.*	NoFire	Ipsdienol				2		
5/13/98	426	plantation	*P. resin.*	NoFire	Ipsenol		29				
5/13/98	427	plantation	*P. resin.*	NoFire	both				11		
5/13/98	427	plantation	*P. resin.*	NoFire	Ipsdienol			2	8		
5/13/98	427	plantation	*P. resin.*	NoFire	Ipsenol		29		1		
5/13/98	429	Disturbed	*P. resin.*	NoFire	both						
5/13/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol	1			1		
5/13/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol		5			1	
5/13/98	430	NearDisturb	*P. resin.*	NoFire	both						
5/13/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
5/13/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol						
5/29/98	401	Undisturbed	*P. resin.*	Fire	both			1	3		
5/29/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol	1		1	23		
5/29/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol	1	2		7		
5/29/98	402	Undisturbed	*P. resin.*	Fire	both			26	7		
5/29/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol						
5/29/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol		39	1			
5/29/98	403	Undisturbed	*P. resin.*	Fire	both				13		
5/29/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol				5		
5/29/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol		2		3		
5/29/98	404	Undisturbed	*P. resin.*	NoFire	both	1			22		
5/29/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	3			11		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
5/29/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		6		
5/29/98	405	Undisturbed	*P. resin.*	NoFire	both				6		
5/29/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	1			14		
5/29/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		7		
5/29/98	406	Undisturbed	*P. resin.*	Fire	both		1		12	2	
5/29/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol	15			44		
5/29/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol		1		6		
5/29/98	407	Undisturbed	*P. resin.*	Fire	both						
5/29/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol				12		
5/29/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
5/29/98	408	Undisturbed	*P. resin.*	Fire	both						
5/29/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol						
5/29/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
5/29/98	409	Undisturbed	*P. resin.*	NoFire	both				3		
5/29/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol						
5/29/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
5/29/98	411	Disturbed	*P. resin.*	Fire	both				21		9
5/29/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol	4	1		23		
5/29/98	411	Disturbed	*P. resin.*	Fire	Ipsenol				13		
5/29/98	412	NearDisturb	*P. resin.*	Fire	both				7		
5/29/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol				8		
5/29/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol				1		
5/29/98	413	Disturbed	*P. resin.*	Fire	both				16		2
5/29/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol	2			4		
5/29/98	413	Disturbed	*P. resin.*	Fire	Ipsenol		4		6		
5/29/98	414	NearDisturb	*P. resin.*	Fire	both				2		
5/29/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol	1					
5/29/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol	2	1			1	
5/29/98	415	Disturbed	*P. resin.*	NoFire	both	1			2		
5/29/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	2					
5/29/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
5/29/98	416	NearDisturb	*P. resin.*	NoFire	both			1	1		
5/29/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	6			1		
5/29/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol		1		1		
5/29/98	417	Disturbed	*P. resin.*	NoFire	both				14		
5/29/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol						
5/29/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol						
5/29/98	418	NearDisturb	*P. resin.*	NoFire	both				13	1	
5/29/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
5/29/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol				1		
5/29/98	419	Disturbed	*P. resin.*	NoFire	both						
5/29/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol						
5/29/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol		3		8	1	
5/29/98	420	NearDisturb	*P. resin.*	NoFire	both	1			3		
5/29/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	8			3		
5/29/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol				3		
5/29/98	421	Undisturbed	Mixed	NoFire	both	1			1		
5/29/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	11				1	
5/29/98	421	Undisturbed	Mixed	NoFire	Ipsenol						
5/29/98	422	Undisturbed	*P strobus*	NoFire	both			1			
5/29/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	1		1	2		
5/29/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol		1		1		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
5/29/98	423	NearDisturb	*P banks*	NoFire	both				9		
5/29/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	4			1		
5/29/98	423	NearDisturb	*P banks*	NoFire	Ipsenol						
5/29/98	424	plantation	*P. resin.*	NoFire	both	2			15		
5/29/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	3			18		
5/29/98	424	plantation	*P. resin.*	NoFire	Ipsenol		1		6		
5/29/98	425	plantation	*P. resin.*	NoFire	both						
5/29/98	425	plantation	*P. resin.*	NoFire	Ipsdienol	1			2		
5/29/98	425	plantation	*P. resin.*	NoFire	Ipsenol				1		
5/29/98	426	plantation	*P. resin.*	NoFire	both						
5/29/98	426	plantation	*P. resin.*	NoFire	Ipsdienol						
5/29/98	426	plantation	*P. resin.*	NoFire	Ipsenol		1		1		
5/29/98	427	plantation	*P. resin.*	NoFire	both				19	3	
5/29/98	427	plantation	*P. resin.*	NoFire	Ipsdienol	5			8		
5/29/98	427	plantation	*P. resin.*	NoFire	Ipsenol		2		2		
5/29/98	429	Disturbed	*P. resin.*	NoFire	both	1	3	3	1		
5/29/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol	1		1	2		
5/29/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
5/29/98	430	NearDisturb	*P. resin.*	NoFire	both	1			2		
5/29/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol			1	8		
5/29/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol				5		
6/17/98	401	Undisturbed	*P. resin.*	Fire	both				1		
6/17/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol				2		
6/17/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol						
6/17/98	402	Undisturbed	*P. resin.*	Fire	both				2	1	
6/17/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	6			1	1	
6/17/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol				4	1	
6/17/98	403	Undisturbed	*P. resin.*	Fire	both	1					
6/17/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol				1		
6/17/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol						
6/17/98	404	Undisturbed	*P. resin.*	NoFire	both				1		
6/17/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	1			1	1	
6/17/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol						
6/17/98	405	Undisturbed	*P. resin.*	NoFire	both	1					
6/17/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol				4		
6/17/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol				3		
6/17/98	406	Undisturbed	*P. resin.*	Fire	both				12		
6/17/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol	1			1		
6/17/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol		1				
6/17/98	407	Undisturbed	*P. resin.*	Fire	both						
6/17/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol						
6/17/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
6/17/98	408	Undisturbed	*P. resin.*	Fire	both				1		
6/17/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol						
6/17/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
6/17/98	409	Undisturbed	*P. resin.*	NoFire	both						
6/17/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol						
6/17/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
6/17/98	411	Disturbed	*P. resin.*	Fire	both						
6/17/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol				4		
6/17/98	411	Disturbed	*P. resin.*	Fire	Ipsenol				1		
6/17/98	412	NearDisturb	*P. resin.*	Fire	both				1		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
6/17/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol						
6/17/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
6/17/98	413	Disturbed	*P. resin.*	Fire	both	1			3	1	
6/17/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol				3		
6/17/98	413	Disturbed	*P. resin.*	Fire	Ipsenol						
6/17/98	414	NearDisturb	*P. resin.*	Fire	both						
6/17/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol						
6/17/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol						
6/17/98	415	Disturbed	*P. resin.*	NoFire	both				2		
6/17/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	3			1		
6/17/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
6/17/98	416	NearDisturb	*P. resin.*	NoFire	both				4		
6/17/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	1			3		
6/17/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol						
6/17/98	417	Disturbed	*P. resin.*	NoFire	both						
6/17/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	1					
6/17/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol		1		11	3	
6/17/98	418	NearDisturb	*P. resin.*	NoFire	both				15		1
6/17/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol				1	1	
6/17/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol				1		
6/17/98	419	Disturbed	*P. resin.*	NoFire	both						
6/17/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol				2		
6/17/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
6/17/98	420	NearDisturb	*P. resin.*	NoFire	both						
6/17/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol				1		
6/17/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
6/17/98	421	Undisturbed	Mixed	NoFire	both						
6/17/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	12					
6/17/98	421	Undisturbed	Mixed	NoFire	Ipsenol		1				
6/17/98	422	Undisturbed	*P strobus*	NoFire	both				1		
6/17/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	1			1		
6/17/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol				1		
6/17/98	423	NearDisturb	*P banks*	NoFire	both						
6/17/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	5					
6/17/98	423	NearDisturb	*P banks*	NoFire	Ipsenol						
6/17/98	424	plantation	*P. resin.*	NoFire	both	2			12		
6/17/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	4			7	1	
6/17/98	424	plantation	*P. resin.*	NoFire	Ipsenol						
6/17/98	425	plantation	*P. resin.*	NoFire	both				2		
6/17/98	425	plantation	*P. resin.*	NoFire	Ipsdienol				1		
6/17/98	425	plantation	*P. resin.*	NoFire	Ipsenol				2		
6/17/98	426	plantation	*P. resin.*	NoFire	both				8	1	
6/17/98	426	plantation	*P. resin.*	NoFire	Ipsdienol				3		
6/17/98	426	plantation	*P. resin.*	NoFire	Ipsenol		1		4		
6/17/98	427	plantation	*P. resin.*	NoFire	both				12		
6/17/98	427	plantation	*P. resin.*	NoFire	Ipsdienol	4			27		
6/17/98	427	plantation	*P. resin.*	NoFire	Ipsenol						
6/17/98	429	Disturbed	*P. resin.*	NoFire	both						
6/17/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol				6		
6/17/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
6/17/98	430	NearDisturb	*P. resin.*	NoFire	both				2	1	
6/17/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol				1		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
6/17/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol				1		
7/1/98	401	Undisturbed	*P. resin.*	Fire	both	1			6		
7/1/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/1/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/1/98	402	Undisturbed	*P. resin.*	Fire	both				1		
7/1/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol				9		
7/1/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol		3		13		
7/1/98	403	Undisturbed	*P. resin.*	Fire	both				8		
7/1/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol	2			9		
7/1/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol		2		2		
7/1/98	404	Undisturbed	*P. resin.*	NoFire	both				3		
7/1/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	31			3		
7/1/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol						
7/1/98	405	Undisturbed	*P. resin.*	NoFire	both				1		
7/1/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	5			3		
7/1/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol						
7/1/98	406	Undisturbed	*P. resin.*	Fire	both						
7/1/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/1/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/1/98	407	Undisturbed	*P. resin.*	Fire	both	1			1		
7/1/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/1/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/1/98	408	Undisturbed	*P. resin.*	Fire	both						
7/1/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/1/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/1/98	409	Undisturbed	*P. resin.*	NoFire	both					1	
7/1/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol						
7/1/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
7/1/98	411	Disturbed	*P. resin.*	Fire	both					1	
7/1/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol				2		
7/1/98	411	Disturbed	*P. resin.*	Fire	Ipsenol						
7/1/98	412	NearDisturb	*P. resin.*	Fire	both						
7/1/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol						
7/1/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
7/1/98	413	Disturbed	*P. resin.*	Fire	both				3		
7/1/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol	9			3		
7/1/98	413	Disturbed	*P. resin.*	Fire	Ipsenol		1				
7/1/98	414	NearDisturb	*P. resin.*	Fire	both						
7/1/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol						
7/1/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol						
7/1/98	415	Disturbed	*P. resin.*	NoFire	both						
7/1/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/1/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/1/98	416	NearDisturb	*P. resin.*	NoFire	both						
7/1/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	32			3		
7/1/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol						
7/1/98	417	Disturbed	*P. resin.*	NoFire	both						
7/1/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/1/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol						

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/1/98	418	NearDisturb	*P. resin.*	NoFire	both				7		
7/1/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
7/1/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol						
7/1/98	419	Disturbed	*P. resin.*	NoFire	both						
7/1/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/1/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/1/98	420	NearDisturb	*P. resin.*	NoFire	both						
7/1/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
7/1/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
7/1/98	421	Undisturbed	Mixed	NoFire	both						
7/1/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	62		1			
7/1/98	421	Undisturbed	Mixed	NoFire	Ipsenol						
7/1/98	422	Undisturbed	*P strobus*	NoFire	both						
7/1/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol						
7/1/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
7/1/98	423	NearDisturb	*P banks*	NoFire	both						
7/1/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	7			1		
7/1/98	423	NearDisturb	*P banks*	NoFire	Ipsenol				1		
7/1/98	424	plantation	*P. resin.*	NoFire	both						
7/1/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	2			1		
7/1/98	424	plantation	*P. resin.*	NoFire	Ipsenol		1				
7/1/98	425	plantation	*P. resin.*	NoFire	both						
7/1/98	425	plantation	*P. resin.*	NoFire	Ipsdienol	3					
7/1/98	425	plantation	*P. resin.*	NoFire	Ipsenol						
7/1/98	426	plantation	*P. resin.*	NoFire	both	3		5	8		
7/1/98	426	plantation	*P. resin.*	NoFire	Ipsdienol				4		
7/1/98	426	plantation	*P. resin.*	NoFire	Ipsenol						
7/1/98	427	plantation	*P. resin.*	NoFire	both				1		
7/1/98	427	plantation	*P. resin.*	NoFire	Ipsdienol						
7/1/98	427	plantation	*P. resin.*	NoFire	Ipsenol						
7/1/98	429	Disturbed	*P. resin.*	NoFire	both						
7/1/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/1/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/1/98	430	NearDisturb	*P. resin.*	NoFire	both						
7/1/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
7/1/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol		2		1		
7/22/98	401	Undisturbed	*P. resin.*	Fire	both						
7/22/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/22/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/22/98	402	Undisturbed	*P. resin.*	Fire	both	4		1	52	1	
7/22/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol				18		
7/22/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol	1	1		18		
7/22/98	403	Undisturbed	*P. resin.*	Fire	both			1	6	1	
7/22/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/22/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/22/98	404	Undisturbed	*P. resin.*	NoFire	both						
7/22/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	2					
7/22/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol	2					
7/22/98	405	Undisturbed	*P. resin.*	NoFire	both	1			5		
7/22/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	1			1		

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/22/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		1		
7/22/98	406	Undisturbed	*P. resin.*	Fire	both						
7/22/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/22/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/22/98	407	Undisturbed	*P. resin.*	Fire	both						
7/22/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/22/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/22/98	408	Undisturbed	*P. resin.*	Fire	both						
7/22/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol						
7/22/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
7/22/98	409	Undisturbed	*P. resin.*	NoFire	both						
7/22/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol						
7/22/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol		1				
7/22/98	411	Disturbed	*P. resin.*	Fire	both						
7/22/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol	6					
7/22/98	411	Disturbed	*P. resin.*	Fire	Ipsenol						
7/22/98	412	NearDisturb	*P. resin.*	Fire	both						
7/22/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol						
7/22/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
7/22/98	413	Disturbed	*P. resin.*	Fire	both						
7/22/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol				1		
7/22/98	413	Disturbed	*P. resin.*	Fire	Ipsenol		1				
7/22/98	414	NearDisturb	*P. resin.*	Fire	both						
7/22/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol						
7/22/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol						
7/22/98	415	Disturbed	*P. resin.*	NoFire	both	1		2	1		
7/22/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/22/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/22/98	416	NearDisturb	*P. resin.*	NoFire	both	22					
7/22/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	4	1		1		
7/22/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol		8		3		
7/22/98	417	Disturbed	*P. resin.*	NoFire	both	6		1	1		
7/22/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	13					
7/22/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/22/98	418	NearDisturb	*P. resin.*	NoFire	both	74		41	5		
7/22/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	1					
7/22/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol						
7/22/98	419	Disturbed	*P. resin.*	NoFire	both				1		
7/22/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/22/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/22/98	420	NearDisturb	*P. resin.*	NoFire	both						
7/22/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
7/22/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
7/22/98	421	Undisturbed	Mixed	NoFire	both						
7/22/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	23					
7/22/98	421	Undisturbed	Mixed	NoFire	Ipsenol	1					
7/22/98	422	Undisturbed	*P strobus*	NoFire	both						
7/22/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	29		1			
7/22/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
7/22/98	423	NearDisturb	*P banks*	NoFire	both				5		
7/22/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	2			1		
7/22/98	423	NearDisturb	*P banks*	NoFire	Ipsenol						

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
7/22/98	424	plantation	*P. resin.*	NoFire	both				4		
7/22/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	1			3		
7/22/98	424	plantation	*P. resin.*	NoFire	Ipsenol						
7/22/98	425	plantation	*P. resin.*	NoFire	both	1					
7/22/98	425	plantation	*P. resin.*	NoFire	Ipsdienol	2					
7/22/98	425	plantation	*P. resin.*	NoFire	Ipsenol						
7/22/98	426	plantation	*P. resin.*	NoFire	both						
7/22/98	426	plantation	*P. resin.*	NoFire	Ipsdienol	12		2			
7/22/98	426	plantation	*P. resin.*	NoFire	Ipsenol		1				
7/22/98	427	plantation	*P. resin.*	NoFire	both						
7/22/98	427	plantation	*P. resin.*	NoFire	Ipsdienol	1			8		
7/22/98	427	plantation	*P. resin.*	NoFire	Ipsenol						
7/22/98	429	Disturbed	*P. resin.*	NoFire	both						
7/22/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol						
7/22/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
7/22/98	430	NearDisturb	*P. resin.*	NoFire	both						
7/22/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol	3			1		
7/22/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol						
8/4/98	401	Undisturbed	*P. resin.*	Fire	both						
8/4/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol						
8/4/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/4/98	402	Undisturbed	*P. resin.*	Fire	both	3		6	16		
8/4/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	1			11		
8/4/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol	1	2		1		
8/4/98	403	Undisturbed	*P. resin.*	Fire	both				2		
8/4/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol				1		
8/4/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/4/98	404	Undisturbed	*P. resin.*	NoFire	both						
8/4/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	8					
8/4/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol						
8/4/98	405	Undisturbed	*P. resin.*	NoFire	both	1					
8/4/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	7			1		1
8/4/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		4		1		
8/4/98	406	Undisturbed	*P. resin.*	Fire	both	7		1			
8/4/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol	26					
8/4/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol		1				
8/4/98	407	Undisturbed	*P. resin.*	Fire	both	4					
8/4/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol	2					
8/4/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/4/98	408	Undisturbed	*P. resin.*	Fire	both				1		
8/4/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol						
8/4/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/4/98	409	Undisturbed	*P. resin.*	NoFire	both						
8/4/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol						
8/4/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol		2				
8/4/98	411	Disturbed	*P. resin.*	Fire	both	1		1			
8/4/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol						
8/4/98	411	Disturbed	*P. resin.*	Fire	Ipsenol						
8/4/98	412	NearDisturb	*P. resin.*	Fire	both						
8/4/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol						

Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
8/4/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
8/4/98	413	Disturbed	*P. resin.*	Fire	both						
8/4/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol	9					
8/4/98	413	Disturbed	*P. resin.*	Fire	Ipsenol						
8/4/98	414	NearDisturb	*P. resin.*	Fire	both	1					
8/4/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol						
8/4/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol						
8/4/98	415	Disturbed	*P. resin.*	NoFire	both						
8/4/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	9					
8/4/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
8/4/98	416	NearDisturb	*P. resin.*	NoFire	both				1		
8/4/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	15			3		
8/4/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol		3		1		
8/4/98	417	Disturbed	*P. resin.*	NoFire	both	4		86	3		
8/4/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	59		25	1		
8/4/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol	1					
8/4/98	418	NearDisturb	*P. resin.*	NoFire	both			1			
8/4/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	6					
8/4/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol		1				
8/4/98	419	Disturbed	*P. resin.*	NoFire	both	1					
8/4/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol	7					
8/4/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
8/4/98	420	NearDisturb	*P. resin.*	NoFire	both						
8/4/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
8/4/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
8/4/98	421	Undisturbed	Mixed	NoFire	both	4			1		
8/4/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	8					
8/4/98	421	Undisturbed	Mixed	NoFire	Ipsenol		2				
8/4/98	422	Undisturbed	*P strobus*	NoFire	both	1			1		
8/4/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	23					
8/4/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
8/4/98	423	NearDisturb	*P banks*	NoFire	both	1					
8/4/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	3					
8/4/98	423	NearDisturb	*P banks*	NoFire	Ipsenol						
8/4/98	424	plantation	*P. resin.*	NoFire	both	3		3			
8/4/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	11			1		
8/4/98	424	plantation	*P. resin.*	NoFire	Ipsenol						
8/4/98	425	plantation	*P. resin.*	NoFire	both						
8/4/98	425	plantation	*P. resin.*	NoFire	Ipsdienol						
8/4/98	425	plantation	*P. resin.*	NoFire	Ipsenol						
8/4/98	426	plantation	*P. resin.*	NoFire	both	1		6			
8/4/98	426	plantation	*P. resin.*	NoFire	Ipsdienol	3					
8/4/98	426	plantation	*P. resin.*	NoFire	Ipsenol	1					
8/4/98	427	plantation	*P. resin.*	NoFire	both						
8/4/98	427	plantation	*P. resin.*	NoFire	Ipsdienol	8			4		
8/4/98	427	plantation	*P. resin.*	NoFire	Ipsenol						
8/4/98	429	Disturbed	*P. resin.*	NoFire	both						
8/4/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol	3			3		
8/4/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						

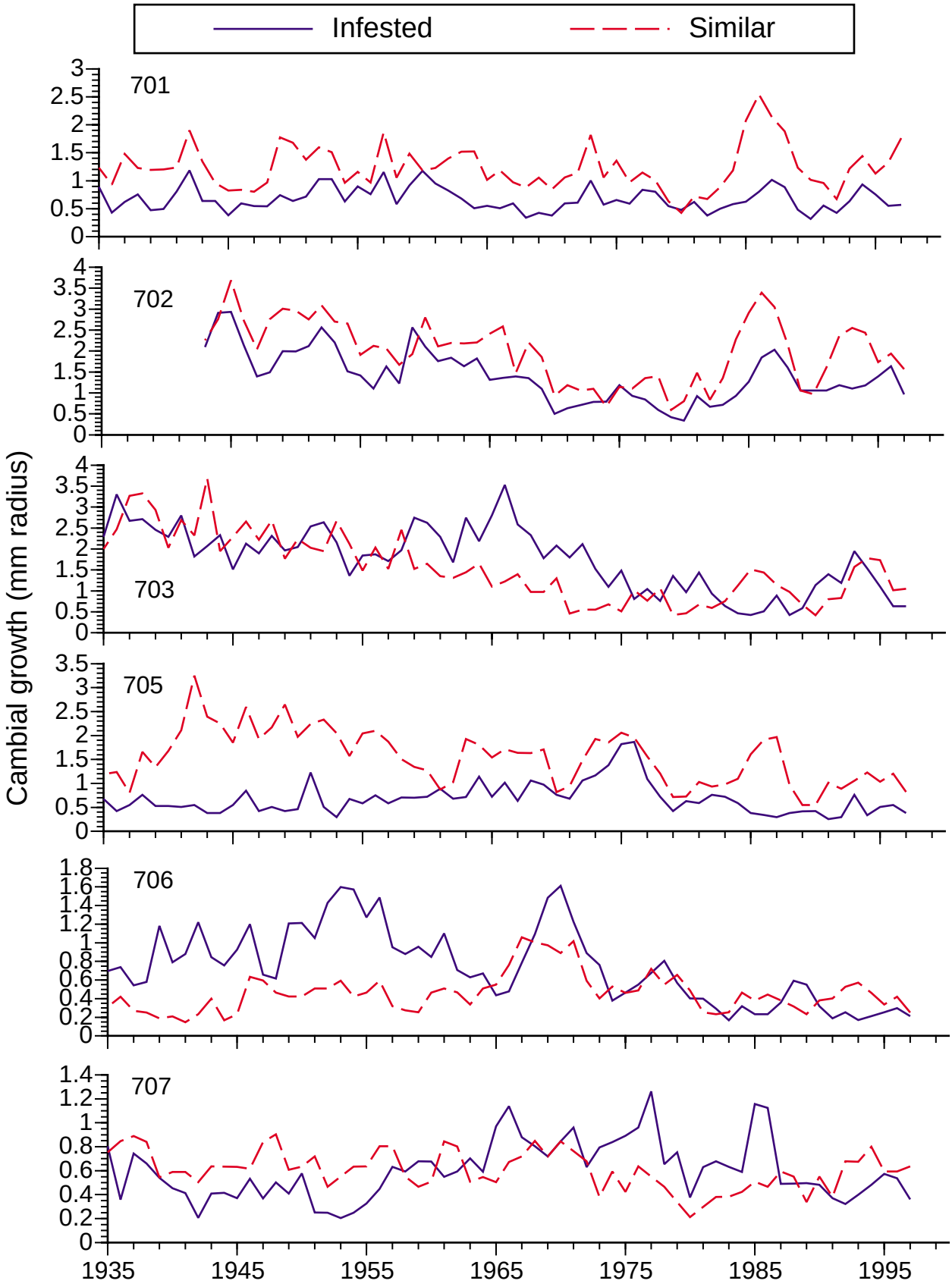
Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
8/4/98	430	NearDisturb	*P. resin.*	NoFire	both	1			5		
8/4/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol				2		
8/4/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol				1		
9/15/98	401	Undisturbed	*P. resin.*	Fire	both						
9/15/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol	25					
9/15/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol		2		1		
9/15/98	402	Undisturbed	*P. resin.*	Fire	both	3				1	
9/15/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	33			3		
9/15/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/15/98	403	Undisturbed	*P. resin.*	Fire	both						
9/15/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol	5			3		
9/15/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/15/98	404	Undisturbed	*P. resin.*	NoFire	both	9					
9/15/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	6					
9/15/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol		1				
9/15/98	405	Undisturbed	*P. resin.*	NoFire	both	4			2		
9/15/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	17			1		
9/15/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		7				
9/15/98	406	Undisturbed	*P. resin.*	Fire	both	2					
9/15/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol	91		2			
9/15/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/15/98	407	Undisturbed	*P. resin.*	Fire	both						
9/15/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol	116		1			
9/15/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol	2					
9/15/98	408	Undisturbed	*P. resin.*	Fire	both						
9/15/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol	9					
9/15/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/15/98	409	Undisturbed	*P. resin.*	NoFire	both	15					
9/15/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	335		5			
9/15/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/15/98	411	Disturbed	*P. resin.*	Fire	both						
9/15/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol	14					
9/15/98	411	Disturbed	*P. resin.*	Fire	Ipsenol		1				
9/15/98	412	NearDisturb	*P. resin.*	Fire	both						
9/15/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol	1					
9/15/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
9/15/98	413	Disturbed	*P. resin.*	Fire	both						
9/15/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol	25					
9/15/98	413	Disturbed	*P. resin.*	Fire	Ipsenol						
9/15/98	414	NearDisturb	*P. resin.*	Fire	both	4					
9/15/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol	4					
9/15/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol		22				
9/15/98	415	Disturbed	*P. resin.*	NoFire	both	12					
9/15/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	26					
9/15/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/15/98	416	NearDisturb	*P. resin.*	NoFire	both	22		3	3		
9/15/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	36			3		
9/15/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol						
9/15/98	417	Disturbed	*P. resin.*	NoFire	both	9		8			
9/15/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol	56			6		
9/15/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/15/98	418	NearDisturb	*P. resin.*	NoFire	both	15			3		

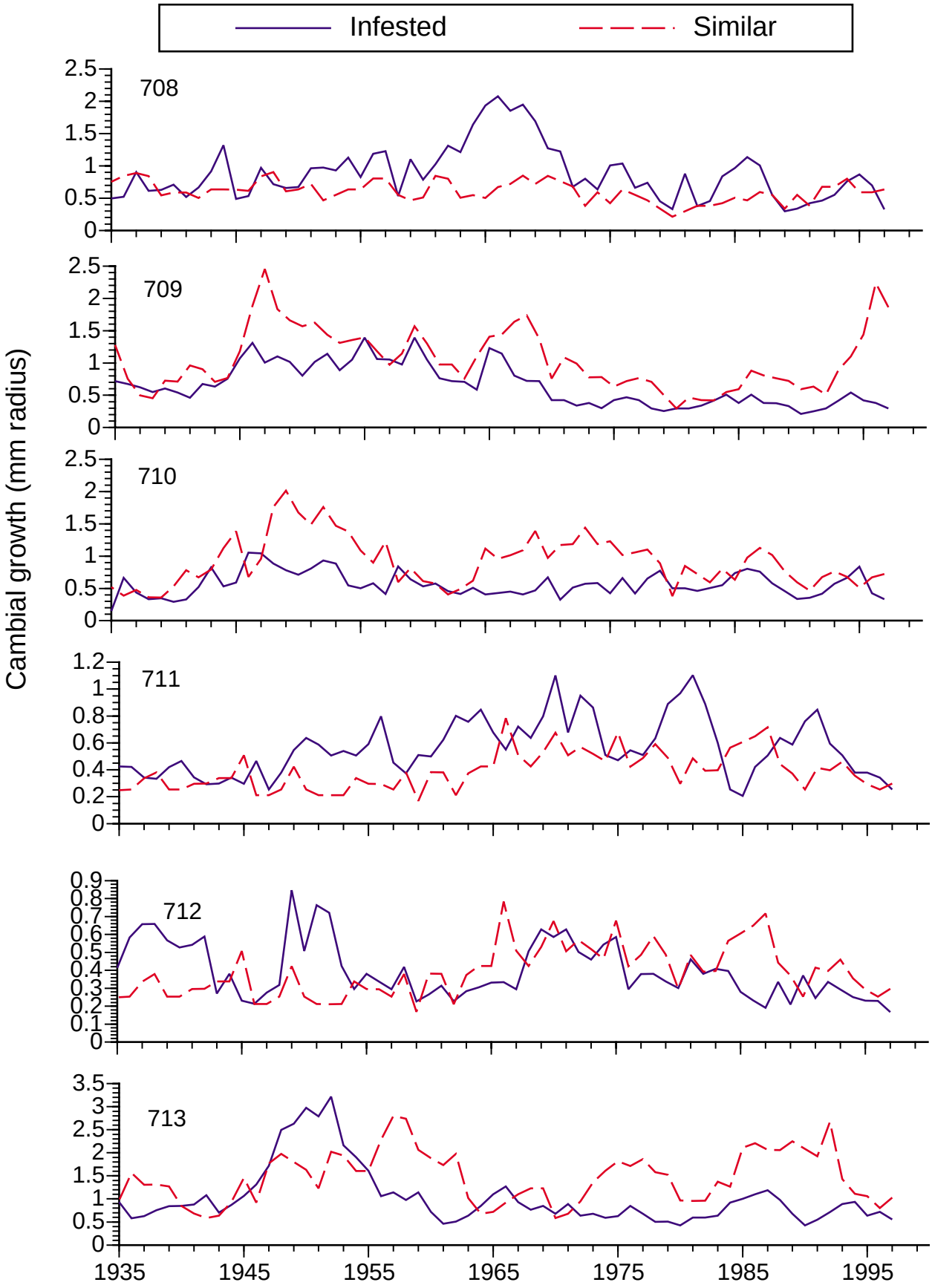
Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
9/15/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	7					
9/15/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol		1				
9/15/98	419	Disturbed	*P. resin.*	NoFire	both				1		
9/15/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol	43		3			
9/15/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/15/98	420	NearDisturb	*P. resin.*	NoFire	both	1					
9/15/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	11					
9/15/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
9/15/98	421	Undisturbed	Mixed	NoFire	both	2					
9/15/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	54					
9/15/98	421	Undisturbed	Mixed	NoFire	Ipsenol	1					
9/15/98	422	Undisturbed	*P strobus*	NoFire	both	1					
9/15/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	29					
9/15/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
9/15/98	423	NearDisturb	*P banks*	NoFire	both	12		1	5		
9/15/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	38		4	2		
9/15/98	423	NearDisturb	*P banks*	NoFire	Ipsenol						
9/15/98	424	plantation	*P. resin.*	NoFire	both	3	1				
9/15/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	64			3	1	
9/15/98	424	plantation	*P. resin.*	NoFire	Ipsenol		41				
9/15/98	425	plantation	*P. resin.*	NoFire	both						
9/15/98	425	plantation	*P. resin.*	NoFire	Ipsdienol						
9/15/98	425	plantation	*P. resin.*	NoFire	Ipsenol	1	1		1		
9/15/98	426	plantation	*P. resin.*	NoFire	both	15					
9/15/98	426	plantation	*P. resin.*	NoFire	Ipsdienol	33		1			
9/15/98	426	plantation	*P. resin.*	NoFire	Ipsenol						
9/15/98	427	plantation	*P. resin.*	NoFire	both	2			2		
9/15/98	427	plantation	*P. resin.*	NoFire	Ipsdienol	6					
9/15/98	427	plantation	*P. resin.*	NoFire	Ipsenol				1		
9/15/98	429	Disturbed	*P. resin.*	NoFire	both	7		1			
9/15/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol						
9/15/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/15/98	430	NearDisturb	*P. resin.*	NoFire	both	4			2		
9/15/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol	6					
9/15/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol						
9/28/98	401	Undisturbed	*P. resin.*	Fire	both	2					
9/28/98	401	Undisturbed	*P. resin.*	Fire	Ipsdienol	11					
9/28/98	401	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	402	Undisturbed	*P. resin.*	Fire	both	4					
9/28/98	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	32					
9/28/98	402	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	403	Undisturbed	*P. resin.*	Fire	both	6					
9/28/98	403	Undisturbed	*P. resin.*	Fire	Ipsdienol	12					
9/28/98	403	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	404	Undisturbed	*P. resin.*	NoFire	both	1					
9/28/98	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	28					
9/28/98	404	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/28/98	405	Undisturbed	*P. resin.*	NoFire	both	3					
9/28/98	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	9			2		
9/28/98	405	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/28/98	406	Undisturbed	*P. resin.*	Fire	both	36			2		
9/28/98	406	Undisturbed	*P. resin.*	Fire	Ipsdienol	53					

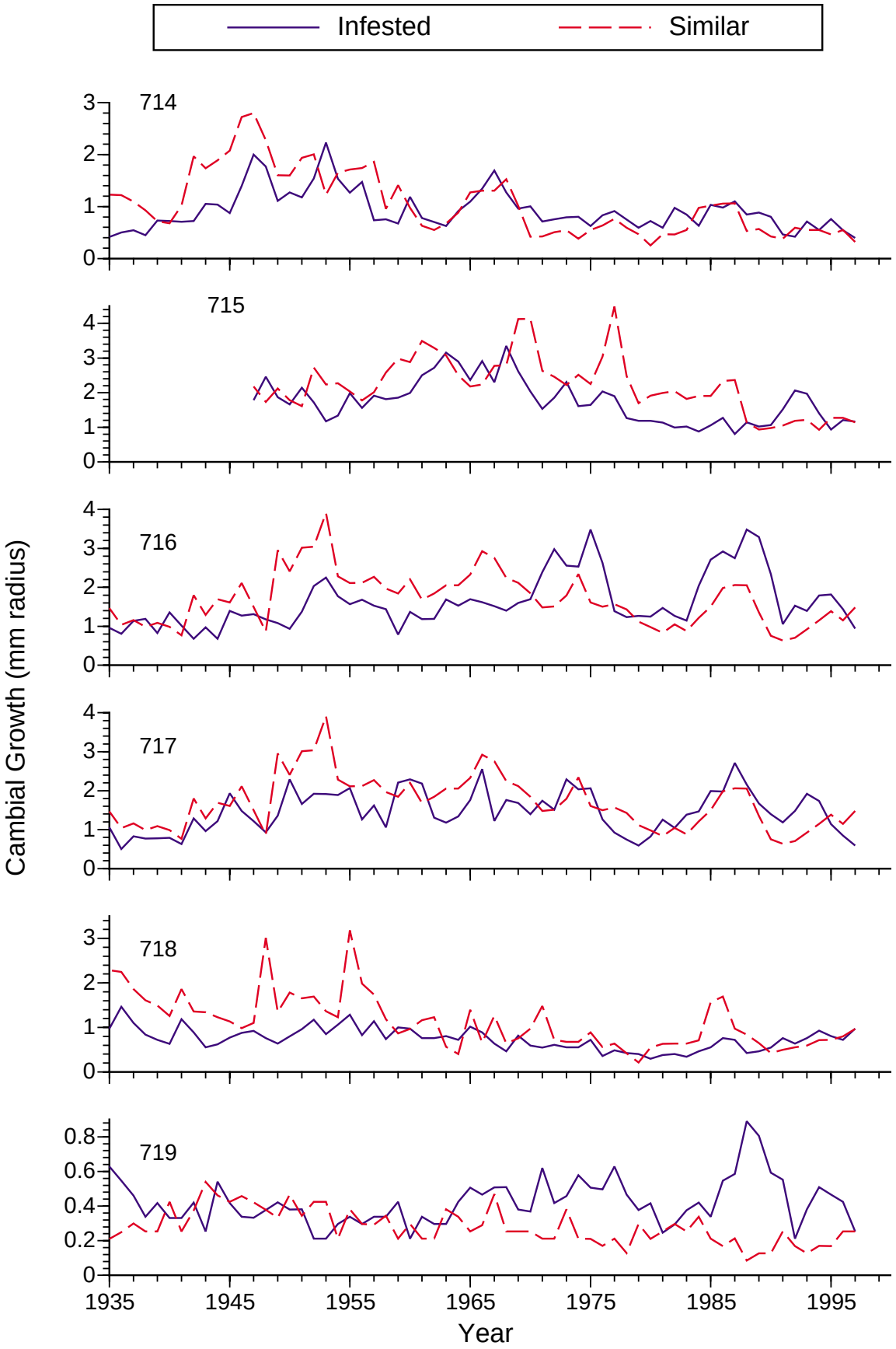
Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
9/28/98	406	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	407	Undisturbed	*P. resin.*	Fire	both	1					
9/28/98	407	Undisturbed	*P. resin.*	Fire	Ipsdienol	16			1		
9/28/98	407	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	408	Undisturbed	*P. resin.*	Fire	both	7					
9/28/98	408	Undisturbed	*P. resin.*	Fire	Ipsdienol	4	1				
9/28/98	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	409	Undisturbed	*P. resin.*	NoFire	both	3					
9/28/98	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	76					
9/28/98	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
9/28/98	411	Disturbed	*P. resin.*	Fire	both	4					
9/28/98	411	Disturbed	*P. resin.*	Fire	Ipsdienol						
9/28/98	411	Disturbed	*P. resin.*	Fire	Ipsenol						
9/28/98	412	NearDisturb	*P. resin.*	Fire	both	2					
9/28/98	412	NearDisturb	*P. resin.*	Fire	Ipsdienol	2					
9/28/98	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
9/28/98	413	Disturbed	*P. resin.*	Fire	both	7					
9/28/98	413	Disturbed	*P. resin.*	Fire	Ipsdienol	4					
9/28/98	413	Disturbed	*P. resin.*	Fire	Ipsenol	1					
9/28/98	414	NearDisturb	*P. resin.*	Fire	both	1					
9/28/98	414	NearDisturb	*P. resin.*	Fire	Ipsdienol	11					
9/28/98	414	NearDisturb	*P. resin.*	Fire	Ipsenol						
9/28/98	415	Disturbed	*P. resin.*	NoFire	both	8			1		
9/28/98	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	2					
9/28/98	415	Disturbed	*P. resin.*	NoFire	Ipsenol	1	1				
9/28/98	416	NearDisturb	*P. resin.*	NoFire	both	3					
9/28/98	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	2					
9/28/98	416	NearDisturb	*P. resin.*	NoFire	Ipsenol		1				
9/28/98	417	Disturbed	*P. resin.*	NoFire	both						
9/28/98	417	Disturbed	*P. resin.*	NoFire	Ipsdienol						
9/28/98	417	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/28/98	418	NearDisturb	*P. resin.*	NoFire	both						
9/28/98	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol	2					
9/28/98	418	NearDisturb	*P. resin.*	NoFire	Ipsenol						
9/28/98	419	Disturbed	*P. resin.*	NoFire	both						
9/28/98	419	Disturbed	*P. resin.*	NoFire	Ipsdienol	13					
9/28/98	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/28/98	420	NearDisturb	*P. resin.*	NoFire	both						
9/28/98	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	28			1		
9/28/98	420	NearDisturb	*P. resin.*	NoFire	Ipsenol	1					
9/28/98	421	Undisturbed	Mixed	NoFire	both	17			1		
9/28/98	421	Undisturbed	Mixed	NoFire	Ipsdienol	49			1		
9/28/98	421	Undisturbed	Mixed	NoFire	Ipsenol	3					
9/28/98	422	Undisturbed	*P strobus*	NoFire	both						
9/28/98	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	32					
9/28/98	422	Undisturbed	*P strobus*	NoFire	Ipsenol						
9/28/98	423	NearDisturb	*P banks*	NoFire	both	1			4		
9/28/98	423	NearDisturb	*P banks*	NoFire	Ipsdienol	6					
9/28/98	423	NearDisturb	*P banks*	NoFire	Ipsenol		1				
9/28/98	424	plantation	*P. resin.*	NoFire	both	4			1		
9/28/98	424	plantation	*P. resin.*	NoFire	Ipsdienol	11					
9/28/98	424	plantation	*P. resin.*	NoFire	Ipsenol						

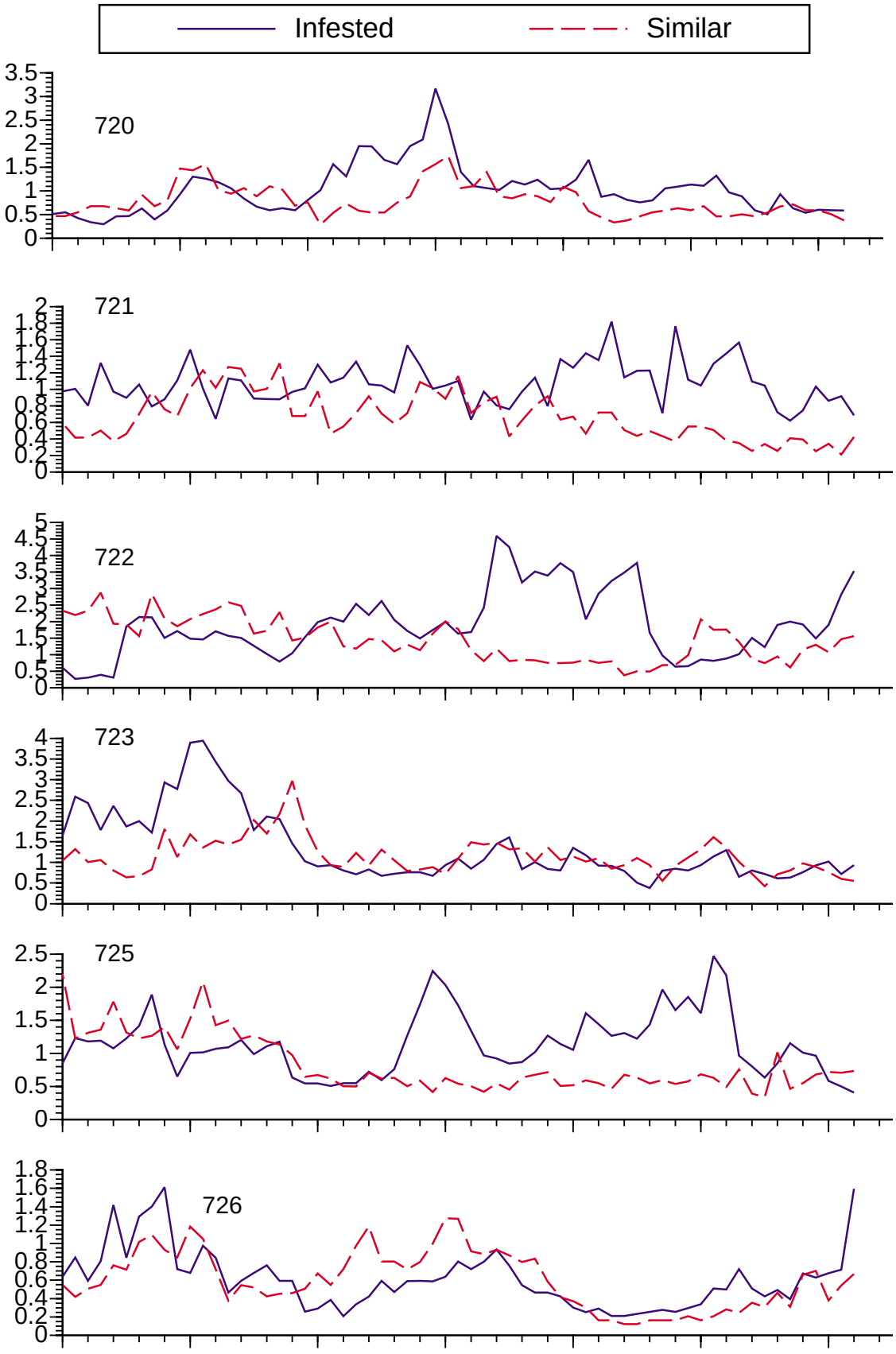
Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
9/28/98	425	plantation	*P. resin.*	NoFire	both	6					
9/28/98	425	plantation	*P. resin.*	NoFire	Ipsdienol	24			3		
9/28/98	425	plantation	*P. resin.*	NoFire	Ipsenol						
9/28/98	426	plantation	*P. resin.*	NoFire	both	2					
9/28/98	426	plantation	*P. resin.*	NoFire	Ipsdienol	4			1	1	
9/28/98	426	plantation	*P. resin.*	NoFire	Ipsenol				1		
9/28/98	427	plantation	*P. resin.*	NoFire	both						
9/28/98	427	plantation	*P. resin.*	NoFire	Ipsdienol	3					
9/28/98	427	plantation	*P. resin.*	NoFire	Ipsenol						
9/28/98	429	Disturbed	*P. resin.*	NoFire	both	3					
9/28/98	429	Disturbed	*P. resin.*	NoFire	Ipsdienol	7					
9/28/98	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
9/28/98	430	NearDisturb	*P. resin.*	NoFire	both	2					
9/28/98	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol	32			3		
9/28/98	430	NearDisturb	*P. resin.*	NoFire	Ipsenol	2					
8/24/99	401	Undisturbed	*P. resin.*	Fire	both						
8/24/99	401	Undisturbed	*P. resin.*	Fire	Ipsdienol	1			1		
8/24/99	401	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/24/99	402	Undisturbed	*P. resin.*	Fire	both	2		1	11		
8/24/99	402	Undisturbed	*P. resin.*	Fire	Ipsdienol	6		1	26		
8/24/99	402	Undisturbed	*P. resin.*	Fire	Ipsenol		5		3		
8/24/99	403	Undisturbed	*P. resin.*	Fire	both				3		
8/24/99	403	Undisturbed	*P. resin.*	Fire	Ipsdienol	12			2		
8/24/99	403	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/24/99	404	Undisturbed	*P. resin.*	NoFire	both						
8/24/99	404	Undisturbed	*P. resin.*	NoFire	Ipsdienol	28		2			
8/24/99	404	Undisturbed	*P. resin.*	NoFire	Ipsenol	1					
8/24/99	405	Undisturbed	*P. resin.*	NoFire	both	1		1	1		
8/24/99	405	Undisturbed	*P. resin.*	NoFire	Ipsdienol	18			3		
8/24/99	405	Undisturbed	*P. resin.*	NoFire	Ipsenol		1		2		
8/24/99	406	Undisturbed	*P. resin.*	Fire	both	13					
8/24/99	406	Undisturbed	*P. resin.*	Fire	Ipsdienol						
8/24/99	406	Undisturbed	*P. resin.*	Fire	Ipsenol	2	1				
8/24/99	407	Undisturbed	*P. resin.*	Fire	both						
8/24/99	407	Undisturbed	*P. resin.*	Fire	Ipsdienol	1					
8/24/99	407	Undisturbed	*P. resin.*	Fire	Ipsenol				1		
8/24/99	408	Undisturbed	*P. resin.*	Fire	both						
8/24/99	408	Undisturbed	*P. resin.*	Fire	Ipsdienol						
8/24/99	408	Undisturbed	*P. resin.*	Fire	Ipsenol						
8/24/99	409	Undisturbed	*P. resin.*	NoFire	both						
8/24/99	409	Undisturbed	*P. resin.*	NoFire	Ipsdienol	11					
8/24/99	409	Undisturbed	*P. resin.*	NoFire	Ipsenol						
8/24/99	411	Disturbed	*P. resin.*	Fire	both						
8/24/99	411	Disturbed	*P. resin.*	Fire	Ipsdienol						
8/24/99	411	Disturbed	*P. resin.*	Fire	Ipsenol						
8/24/99	412	NearDisturb	*P. resin.*	Fire	both				1		
8/24/99	412	NearDisturb	*P. resin.*	Fire	Ipsdienol	8					
8/24/99	412	NearDisturb	*P. resin.*	Fire	Ipsenol						
8/24/99	413	Disturbed	*P. resin.*	Fire	both						
8/24/99	413	Disturbed	*P. resin.*	Fire	Ipsdienol						
8/24/99	413	Disturbed	*P. resin.*	Fire	Ipsenol		3				
8/24/99	414	NearDisturb	*P. resin.*	Fire	both						

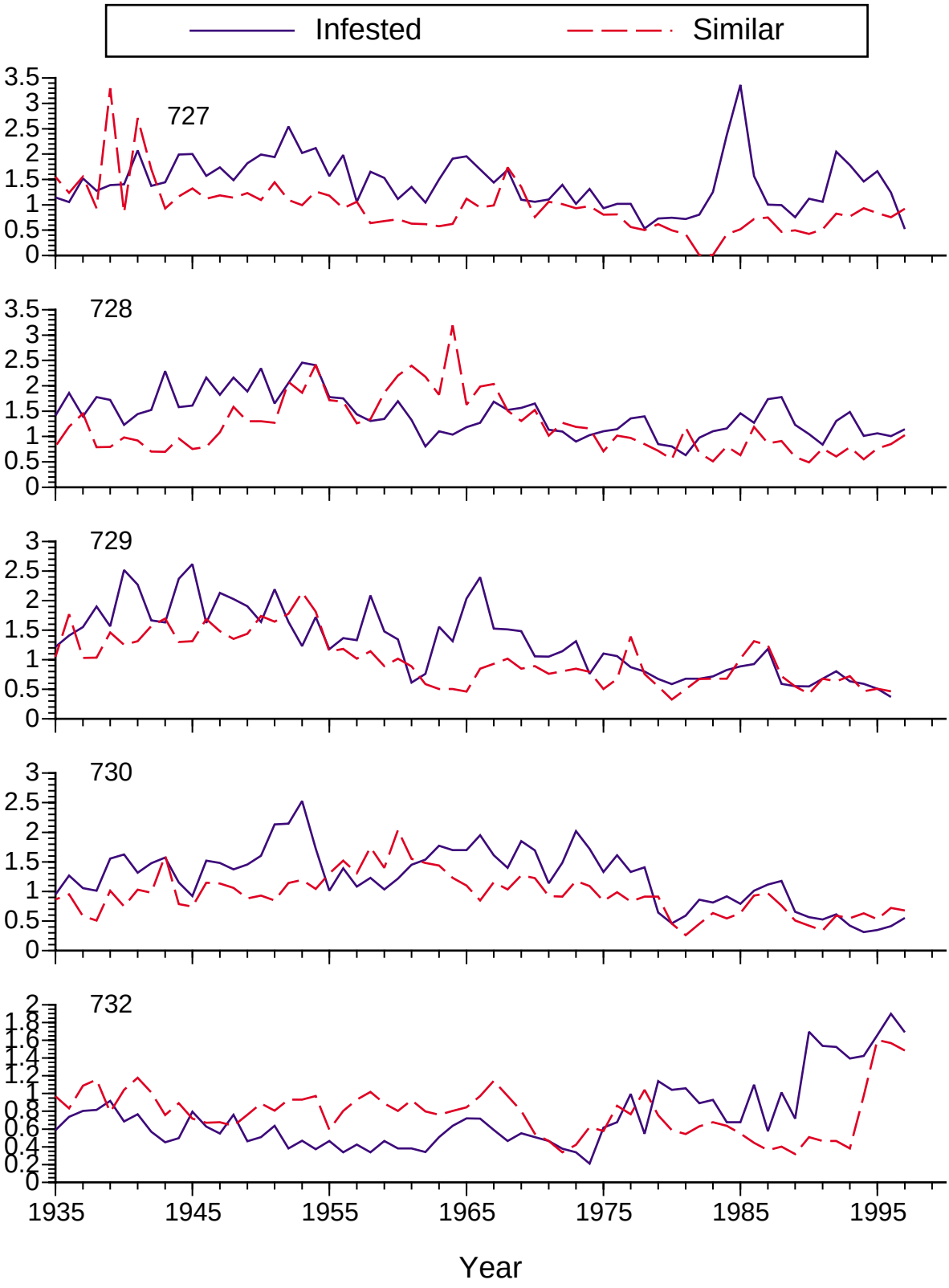
Date	Site ID	Stand type	Tree spp.	Fire in '98	Lure	*I. pin*	*I. gr.*	*I. per.*	*T. dub.*	*P. cyl*	*P. par.*
8/24/99	414	NearDisturb	*P. resin.*	Fire	Ipsdienol						
8/24/99	414	NearDisturb	*P. resin.*	Fire	Ipsenol						
8/24/99	415	Disturbed	*P. resin.*	NoFire	both						
8/24/99	415	Disturbed	*P. resin.*	NoFire	Ipsdienol	43		1			
8/24/99	415	Disturbed	*P. resin.*	NoFire	Ipsenol						
8/24/99	416	NearDisturb	*P. resin.*	NoFire	both	2		5	1		
8/24/99	416	NearDisturb	*P. resin.*	NoFire	Ipsdienol	1		3	2		
8/24/99	416	NearDisturb	*P. resin.*	NoFire	Ipsenol	1	2	1			
8/24/99	417	Disturbed	*P. resin.*	NoFire	both						
8/24/99	417	Disturbed	*P. resin.*	NoFire	Ipsdienol						
8/24/99	417	Disturbed	*P. resin.*	NoFire	Ipsenol						
8/24/99	418	NearDisturb	*P. resin.*	NoFire	both	7		82	1		
8/24/99	418	NearDisturb	*P. resin.*	NoFire	Ipsdienol						
8/24/99	418	NearDisturb	*P. resin.*	NoFire	Ipsenol		7	2	1		
8/24/99	419	Disturbed	*P. resin.*	NoFire	both						
8/24/99	419	Disturbed	*P. resin.*	NoFire	Ipsdienol						
8/24/99	419	Disturbed	*P. resin.*	NoFire	Ipsenol						
8/24/99	420	NearDisturb	*P. resin.*	NoFire	both						
8/24/99	420	NearDisturb	*P. resin.*	NoFire	Ipsdienol	1					
8/24/99	420	NearDisturb	*P. resin.*	NoFire	Ipsenol						
8/24/99	421	Undisturbed	Mixed	NoFire	both						
8/24/99	421	Undisturbed	Mixed	NoFire	Ipsdienol	258		1			
8/24/99	421	Undisturbed	Mixed	NoFire	Ipsenol		4		1		
8/24/99	422	Undisturbed	*P strobus*	NoFire	both						
8/24/99	422	Undisturbed	*P strobus*	NoFire	Ipsdienol	5					
8/24/99	422	Undisturbed	*P strobus*	NoFire	Ipsenol		3				
8/24/99	423	NearDisturb	*P banks*	NoFire	both	2			1		
8/24/99	423	NearDisturb	*P banks*	NoFire	Ipsdienol	24			5		
8/24/99	423	NearDisturb	*P banks*	NoFire	Ipsenol		1				
8/24/99	424	plantation	*P. resin.*	NoFire	both						
8/24/99	424	plantation	*P. resin.*	NoFire	Ipsdienol	15					
8/24/99	424	plantation	*P. resin.*	NoFire	Ipsenol		12		4	1	
8/24/99	425	plantation	*P. resin.*	NoFire	both	2				1	
8/24/99	425	plantation	*P. resin.*	NoFire	Ipsdienol						
8/24/99	425	plantation	*P. resin.*	NoFire	Ipsenol					1	
8/24/99	426	plantation	*P. resin.*	NoFire	both				1		
8/24/99	426	plantation	*P. resin.*	NoFire	Ipsdienol	16			1		
8/24/99	426	plantation	*P. resin.*	NoFire	Ipsenol		6		1		
8/24/99	427	plantation	*P. resin.*	NoFire	both						
8/24/99	427	plantation	*P. resin.*	NoFire	Ipsdienol	1			3		
8/24/99	427	plantation	*P. resin.*	NoFire	Ipsenol		2		2		
8/24/99	429	Disturbed	*P. resin.*	NoFire	both						
8/24/99	429	Disturbed	*P. resin.*	NoFire	Ipsdienol						
8/24/99	429	Disturbed	*P. resin.*	NoFire	Ipsenol						
8/24/99	430	NearDisturb	*P. resin.*	NoFire	both						
8/24/99	430	NearDisturb	*P. resin.*	NoFire	Ipsdienol	6					
8/24/99	430	NearDisturb	*P. resin.*	NoFire	Ipsenol						

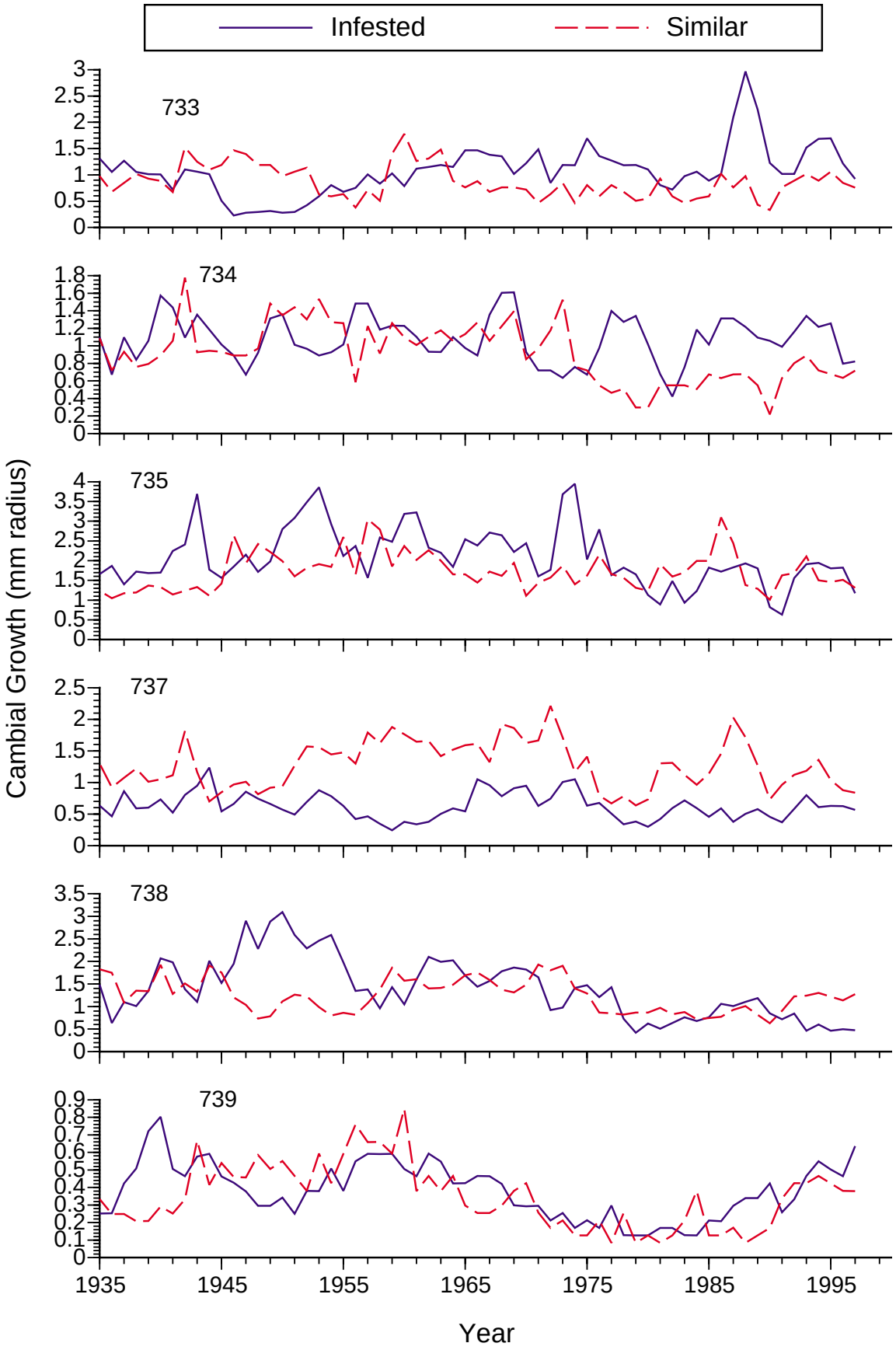

Infested
Similar
701
702
703
705
706
707
Cambial growth (mm radius)
1935
1945
1955
1965
1975
1985
1995


Infested
Similar
Cambial growth (mm radius)
708
709
710
711
712
713
1935
1945
1955
1965
1975
1985
1995


Infested
Similar
714
715
716
717
718
719
Cambial Growth (mm radius)
Year
1935
1945
1955
1965
1975
1985
1995


Infested
Similar
720
721
722
723
725
726


Infested
Similar
727
728
729
730
732
1935
1945
1955
1965
1975
1985
1995
Year


Infested
Similar
733
734
735
737
738
739
Cambial Growth (mm radius)
Year
1935
1945
1955
1965
1975
1985
1995